THE SINGING BEHAVIOUR OF COAL TITS (PARUS ATER)

Asep Sunjaya Adhikerana

A Thesis Submitted for the Degree of PhD
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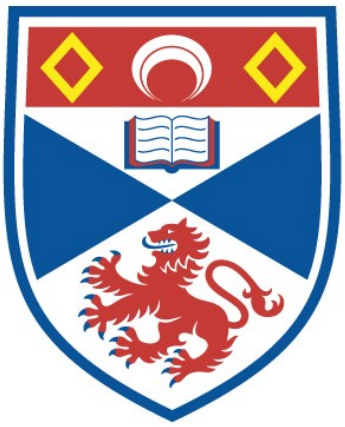

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by

Asep Sunjaya Adhikerana

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for the degree of Doctor of Philosophy.

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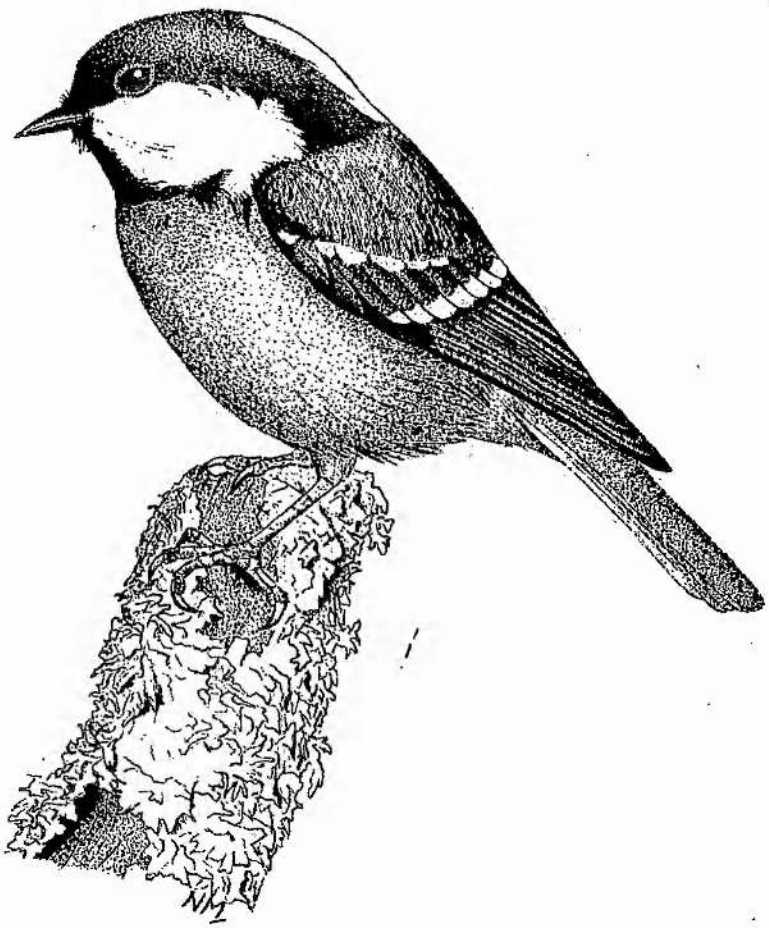

CONTENTS

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(a) I, Asep Sunjaya Adhikerana, hereby certify that this thesis has been composed by myself, that it is a record of my own work, and it has not been accepted in partial or complete fulfilment of any other degree of professional qualification.

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ABSTRACT

This thesis investigates the singing behaviour of coal tits (*Parus ater*) from two different study sites. A background to the functional significance of songs in a broad context is given in Chapter 1. This chapter also briefly introduces the biology of coal tits.

Chapter 2 describes more general aspects of coal tit songs, and evaluates and compares the variability in song structure of two coal tit populations.

The study has looked at the distribution of songs within populations, and at the effect of distance between individuals on the composition of their repertoires. The results are presented in Chapter 3.

A new hypothesis has been proposed to explain the significance of song repertoires, namely the anti-exhaustion hypothesis. The hypothesis was tested on coal tits, and the results are presented in Chapter 4.

Using playback experiments the singing interaction in coal tits was investigated. Two experiments were carried out in order to test the predictions that a bout of song could give information about individual's fitness, and that song length might indicate individual 'strength'. The results are presented in Chapter 5.

CHAPTER 1.

GENERAL INTRODUCTION AND OUTLINE OF THE THESIS

INTRODUCTION

This thesis examines general aspects of the singing behaviour of coal tits (*Parus ater*), ranging from description of song structure, song distribution within populations, singing performance and interaction with external stimuli. This chapter will introduce some aspects of songs as a means of communication, and describe briefly the biology and behaviour of coal tits. Later, the outline of the thesis will also be described.

Bird song has been of interest to humans since long before the emergence of ethology. Armstrong (1969) describes the association of bird sound and man in many ancient societies from Europe to the Far East. He quotes how bird vocalization had been used as the source of art by early man. For the last three decades bird song has been a key subject of behavioural study aimed at understanding evolutionary or ecological aspects of bird life, and most recently at uncovering brain mechanisms.

Biological aspects encompassed by studies of bird song range from habitat adaptation, to reproductive behaviour and the dynamics of populations. Not only does specific adaptation to habitats involve the evolution of appropriate morphological features and individual and/or social behaviour of a species, but also appropriate vocal characteristics. Reproduction is obviously a very important aspect of bird life since this process determines the individual's contribution to the next generation. Two major aspects of bird reproduction which involve songs are territorial establishment and mate attraction. Both involve competition between conspecifics. Interspecific competition rarely, if ever, occurs for

reproductive purposes but there may be territorial competition where two or more species compete for resources available in a particular territory.

Songs and habitat adaptation.-- Song is a means of communication. For such communication to be effective the song must be transmitted through the environment which consists of the habitat of the species. The acoustic characteristics of habitats affect the attenuation or propagation of the transmitted signals (Marten & Marler 1977, Hansen 1978), and eventually they act as selective pressures on the signals transmitted by the birds (Morton 1975).

Morton (1975) suggested that birds would exploit optimum frequencies for singing depending on the habitats where they live. In tropical forested habitats songs tend to be lower pitched and with a narrower range of frequencies than those in open habitats (Morton 1975). Birds in temperate forested habitats are more likely to sing songs with lower frequencies than those living in an open habitat (Wasserman 1979). Aylor (1972), however, found little difference in the attenuation patterns of hemlock, pine and mixed deciduous habitats for transmission at frequencies of 2 - 10 KHz. Birds living in marsh habitats, where the ground effect is negligible, have songs with lower frequency than those in grassland habitats (Cosens & Falls 1984).

The songs of great tits have been found to be different in different habitat types such as forests and more open parkland woods (Hunter & Krebs 1979). Hunter & Krebs (1979) suggested that such differences were partly related to differences in acoustic transmission between habitats. They

did not find any association between acoustic characteristics of great tit songs and climatic condition, body size, perch height or acoustic competition. However, they suggested that territory size might be related to song characteristics in this species.

Forest birds with large territories might have to sing songs with good transmission. Here, the distance between communicating birds may play a role. Some authors (e.g. Konishi 1970, Nottebohm 1975, Zann 1975) have suggested that distance between birds is likely to be an important factor that affects the structure of songs. Because songs with low frequencies will transmit further in the forested habitats than those with high frequencies, larger territories should favour lower frequency songs. To what extent such factors as territory size and the distance between communicating birds are important in the form of songs of other *Parus* species is still little known.

Climatological factors such as temperature, humidity and wind will certainly affect sound propagation. Although Hunter & Krebs (1979) did not find any effect of temperature and humidity on the transmission of great tit songs, these factors may still play a role in other species. An increase in temperature will make sound travel faster, and the sound will be less attenuated at higher humidity (Harris 1966, 1969). Sound attenuation is also determined by the wind. Sounds with higher frequencies are more affected than those with lower frequencies (Ingard 1953).

The ground effect is also considered to be an important factor in determining sound transmission. Not only does the ground absorb sound but it also reflect sound waves. The

magnitude of the ground effect depends on the soil's porosity (Piercy *et al.* 1977), and the interference of sound waves is dependent upon the heights of both the source and receiver (Embleton *et al.* 1976). Roberts *et al.* (1981), however, doubted the influence of the ground effect on the birds' songs sung between one and ten meters above the ground, within a distance of less than about 100 meters from the receiver, and with frequencies of more than 500 Hz. Martin (1981) suggested that differences in the ground effect may occur between habitats with different plant communities.

The density of avian communities within a habitat may also be a source of acoustic interference. Sorjonen (1986) found a strong effect of avian densities on the song length of some European passerines. Lehtonen (1983) found a decrease in the length of great tit songs which was associated with an increase in environmental noise. He suggested that changes in the syllable patterns of great tit songs were an adaptation to changes in the acoustic characters of habitats. Birds may avoid such interference by singing at a time when other birds are silent (Cody & Brown 1969).

Specific characteristics of habitats, such as the presence of waterfalls, may generate noticeable background noise which may affect the shaping of birds' vocalizations. Martens (1990) found that birds living near Himalayan torrents avoided vocalizations with low frequencies; the calls and songs were concentrated in a frequency range of 4 - 6.5 KHz. Habitat structures as well as avifaunal density may be important factors in determining the background noise within a habitat.

Songs and reproduction.-- To date the most acknowledged functions of song in passerine birds are in rival repulsion and mate attraction, both of them of course related to the birds' reproduction. Experiments have provided evidence for the role of song in defending a territory from which the results suggested that song alone is sufficient to deter other males from settling in the territory (e.g. Krebs 1976, 1977, Krebs *et al.* 1978, Yasukawa 1981).

The number of different song types within a bird's repertoire also plays an important role in defending territories, where birds with larger repertoires have been found more successful in defending their territories (Krebs 1976, Krebs *et al.* 1978), and in acquiring better quality territories (Howard 1974).

Evidence for the function of song in mate attraction has also been found in many species. In budgerigars (*Melopsittacus undulatus*), Brockway (1965) examined the effect of playback of male vocalizations on egg-laying in females. This showed that the male vocalizations function to stimulate egg production in females. In the sedge warbler (*Acrocephalus schoenobaenus*), Catchpole (1977) showed that males responded more strongly to playback of songs before pairing than to those carried out after pairing. Indirectly, this showed that song was used primarily for female attraction. Yasukawa *et al.* (1980) also found in red-winged blackbirds (*Agelaius phoeniceus*) that males with larger repertoires could obtain more females.

The variety of songs has also been found to correlate with success in attracting mates and stimulating them once attracted. Howard (1974) found that male mockingbirds (*Mimus polyglottos*) with more elaborate songs mated earlier than

those with simpler songs. Male sedge warblers with more complicated songs within their repertoires were able to attract females earlier than those with simpler ones (Catchpole 1980). However, McGregor *et al.* (1981) did not find any correlation between repertoire size (i.e. the number of different song types) in great tits and timing of breeding or number of offspring produced, although they found that males with larger repertoires were more likely to breed in a second season and to father offspring which survived to breed.

The role of repertoire size has been discussed extensively elsewhere (e.g. Krebs 1977, Krebs & Kroodsma 1982, and briefly in Chapter 5). One of the advantages of having a repertoire may be that males will be able to match the songs of neighbouring and/or rival males. Payne (1982), for example, found in indigo buntings (*Passerina cyanea*) that individuals that were able to match their neighbours' songs had significantly greater mating success, nesting success and fledging success than those that were unable to match the songs of neighbouring birds.

Apart from repertoire size, characteristics of songs are also considered to be important in mate choice (e.g. Wasserman 1977, Lambrechts & Dhondt 1986, 1987). In great tits, song length has been suggested as a signal of male quality (Lambrechts & Dhondt 1986, 1987). In this species, Lambrechts & Dhondt (1986) found significant correlations between song length and a measure of reproductive success. They suggested that song length gives information about the quality of the singer (Lambrechts & Dhondt 1987). Bijnens (1988) suggested that the song length of blue tits might reflect singing capacity but the males with longer songs were not found to

have a greater reproductive success although they survived better than those with shorter songs. McGregor (1988) tested the idea that the song length used in spontaneous singing was a signal of male quality in chiffchaffs (*Phylloscopus collybita*) using playback experiments. His prediction was that if song length indicated male quality to rivals during aggressive encounters, playback would elicit longer songs. He found no obvious effects of playback on song length of this species, and questioned whether song length was a simple indicator of male quality.

Songs and populations.-- Bird song has been viewed as a cultural tradition among individuals (reviewed by Mundinger 1982, Kroodsma & Baylis 1982), and is culturally transmitted from one individual to another within populations (Slater & Ince 1979, Payne *et al*. 1981, Slater 1986, Baker & Jenkins 1987). The cultural transmission of song is facilitated by imitative learning (Payne *et al*. 1981). Young males may learn the songs from older males within their home area if they do not disperse (Marler & Tamura 1964) or copy the songs from others after they dispersed from their natal sites (Kroodsma 1974, Jenkins 1978).

In white-crowned sparrows (*Zonotrichia leucophrys*), Marler & Tamura (1962) reported dialects as song traditions within populations. They assumed that population membership stayed much the same through time, yet the fluctuations of population members may affect song tradition. Surviving young that learn songs from adults and then disperse further away from their natal area may introduce new songs into the population where they breed, or they may learn new songs from

neighbouring birds at their breeding sites. The dipersal of young birds and the extent of their accuracy in song copying both before and after dispersal may eventually influence song distribution within the population. When this happens across generations, it might result in changes in song within a population from time to time.

Payne *et al.* (1981) have demonstrated such changes in populations of indigo buntings (*Passerina cyanea*) for several generations. Most of the songs recorded in the 1960's were no longer found 15 years later, and they suggested that such disappearance from the population was due to cultural drift that altered the songs beyond recognition. They found that the survival rate of adult birds was much smaller than the survival rate of their songs, and they suggested that local songs in this species were relatively long-lived behaviour traditions and persisted due to song learning across generations independent on kinship between birds.

The changes of songs within populations across time had been reported earlier for saddlebacks (*Philesturnus carunculatus*) and chaffinches (*Fringilla coelebs*). Jenkins (1978) found changes in the songs of saddleback populations through time, and such changes occurred when young birds modified songs which they learnt from other birds. Ince *et al.* (1980) compared the songs of a chaffinch population recorded in 1960 with those recorded at the same area in 1978. They found that most of the song types recorded in 1960 had disappeared or changed beyond recognition, and only a small number of song types had remained identical across this period. The similarity in song over time may indicate local

song traditions that have undergone little modification in song copying (Slater *et al.* 1980).

Song changes within populations have also been reported in great tits. McGregor & Krebs (1989) carried out a study on great tits from 1975 to 1984 inclusive, and compared the changes in repertoire composition with age and changes in neighbourhood. They found that changes in repertoire composition were a common feature of great tit repertoires, and such changes did not correlate with age but with changes in neighbours. The songs added to an individual's repertoire were similar to those of newly arrived neighbours.

Although these studies did not directly measure the relation between the dynamics of a population, at least as far as the departure of population members and arrivals of new members are concerned, with the changes in song distribution within the population, it seems likely that these two aspects of population dynamics along with the accuracy or inaccuracy of song copying by the population members affect the song composition within the population.

BIOLOGY AND BEHAVIOUR OF COAL TITS.

There are 58 species currently recognized in the family Paridae, and 42 of them belong to the true tits, sub-family Parinae. The distribution of these tits is throughout the northern hemisphere and Africa, but they are not found in South America or Australia (Paynter 1967). Some of the true tits have a very extensive range. Great tits (*Parus major*), for example, occur in woodland habitats from Ireland to Japan and from Siberian forest to southeast Asia (Paynter 1967). The

distribution of coal tits (*Parus ater*), in Europe, extends from Scandinavia southwards to southern Europe and southeastwards to the Balkans (Perrins 1979).

Seven species of tits occur in Britain : coal tit (*Parus ater*), great tit (*P.major*), blue tit (*P.caeruleus*), crested tit (*P.cristatus*), marsh tit (*P.palustris*), willow tit (*P. montanus*) and long-tailed tit (*Aegithalos caudatus*). The coal, great and blue tits are widespread in Britain, whereas the crested tits are confined to the north of Scotland and the marsh and willow tits are more confined to habitats in England (Perrins 1979).

The British tits have been studied comprehensively with regard to population ecology (reviewed by Lack 1966 and Perrins 1979). Niche differentiation between these tits has also been studied (e.g. Hartley 1953, Gibb 1954, Betts 1955). Snow (1954) has reviewed the habitat selection and behaviour of Eurasian tits. On vocal communication, Gompertz (1961) studied the vocal vocabulary of the great tit and its relatives. Later, Latimer (1977) compared the structures of songs and calls of some *Parus* species, and recently, Hailman (1989) reviewed the vocal organization of all the Paridae.

Habitat type.-- The main habitat of coal tits is generally coniferous woodland, although they are also present in broad-leaved deciduous woods. Perrins (1979) suggested that in other parts of Europe the coal tit seems to prefer spruce to pinewoods, and quoted Löhrl (1974) who found that in Germany the average breeding density is about a pair per hectare, which is roughly three times the normal rate reached in Britain. In Marley wood, a broad-leaved deciduous area of 27

hectares (about 67 acres), only one or two pairs of coal tits were found, whereas in pinewoods coal tits can be found at a density of as much as one pair per eight acres (Lack 1966).

Between coal tits that inhabit broad-leaved and coniferous woods there is a morphological difference, particularly in the beak shape (Snow 1954). Coal tits in coniferous forest were found to have longer and thinner beaks than those inhabiting deciduous woods. Such a difference might be attributed to the need to probe amongst needles where small insects or seeds are hidden. Snow also recorded that insects taken by coal tits living in conifers were smaller than those taken by coal tits in deciduous woods.

Feeding habits.-- Tits feed on small seeds and insects. Coal tits were found to prey on smaller insects and feed on smaller seeds than blue, great and marsh tits (Betts 1955). As mentioned earlier, the beak shape of coal tits has become specialized for smaller food items. When foraging in trees coal tits were found to use feeding stations higher than other tits (Gibb 1954). Being smaller than the others, coal tits take less food than either great or blue tits but they require more energy in proportion to their body size (Gibb 1957). This may force them to search for food more than the others. Gibb (1954), for example, has revealed that the proportion of time spent feeding by coal tits was higher than great or blue tits throughout the year.

Coal tits regularly store food (Hart 1958). Richards (1949, 1958) found that they stored large quantities of seeds in the same areas as those in which they foraged, particularly among the needles, behind the bark of trees or in the ground.

Compared to other tits that store food, such as crested, willow and marsh tits, coal tits tend to store higher in the tree (Perrins 1979). Hoarding may help them to survive through the winter when the food becomes scarcer.

The scarcity of food during the winter becomes greater as the season progresses because the seeds produced in autumn tend to diminish in quantity and very few insects breed or grow in that season. The need for food storing seems very important to coal tits. Gibb (1960) has suggested that food shortage during winter might lead to a decline in the number of coal tits through the winter.

Coal tits are believed to be largely sedentary. Local movement within Britain occasionally occurs but European coal tits are often found to be migratory within the continent, and such movements are thought to be largely due to food shortage (Scherrer 1972, Perrins 1979). Cramp *et al.* (1960) noted that very large numbers of coal, great and blue tits occasionally took part in irruptive movements into Britain, and these movements occurred when the food supply was short and there were large numbers of tits.

Breeding.-- Most tits roost in natural holes or dense foliage. Nesting boxes are also often used for roosting. Males and females normally do not roost together, and the females often breed in the sites where they roost (Perrins 1979). In tits both sexes explore prospective nesting-sites, and during the period of searching and selecting nesting-sites in crested and willow tits special prospecting displays are given (Nethersole-Thompson & Nethersole-Thompson 1943). Blue tits were found to show courtship displays during this period,

when a male finds a nesting site and attracts a female to it (Stokes 1960).

Coal tits commonly nest low down in rotten stumps or burrows (Hayman & Burton 1976). As in most of the tits, nest-building is carried out by the female and during this period the female is dominant over the male (Perrins 1979). The female usually forms a nest cup of moss lined by other materials such as hair and fur, and she may take several days to complete nest-building (Perrins 1979).

During the laying period the female usually roosts in the nest overnight and lays her eggs early in the morning before leaving (Pullen 1946). Egg-laying is usually done every day until the clutch is complete; the clutch size in coal tits is typically 7 - 12 eggs (Hayman & Burton 1976). When the clutch is completed the female usually starts the incubation. In all tit species the length of incubation period is similar at about fourteen days (Perrins 1979). In great tits, Royama (1966) found that females which incubated their eggs more attentively would hatch them earlier. The survival rate of young birds varies between species as well as between individuals. In great tits, the survival of young depends on their weight when they leave the nest (Bulmer & Perrins 1973).

As in other tits, both coal tit parents rear young. The young birds may be seen with the parents for several weeks after they have left the nest (Perrins 1979). The average survival rate of adult great tits is, annually, about 50 %, and this may be similar to other tits including coal tits (Bulmer & Perrins 1973).

Communication.-- Most tits of which the vocalizations have been described are very vocal birds (e.g. Gompertz 1961, Krebs 1976, Latimer 1977, Göller 1987, Rost 1988, Hailman 1989). Göller (1987) has described the songs and calls of coal tits in Germany and their possible communicative functions.

The song is, as in many other song birds, associated with territorial activities and is mainly given by the males (Gompertz 1961, Göller 1987). Most tits sing more than one version of their species-specific song. Male great tits may have at least four different song types (Gompertz 1961), and coal tits may have up to 12 song types in their repertoires (Göller 1987).

Calls are often associated with various situations with different ones delivered in different contexts (Catchpole 1979), such as begging calls given by young birds, contact calls between juveniles and the parents, warning calls when confronted by intrusion, or alarm calls which are given under conditions of danger.

Göller (1987) described a series of calls in coal tits which were associated with the contexts mentioned above. As in other tits, coal tits use courtship calls when attracting females (Latimer 1977, Göller 1987). Warning calls are often given to discourage other birds from being too close (Gompertz 1961). Further, Gompertz (1961) listed no less than six great tit calls associated with situations of danger.

When giving warning calls, tits usually display threat postures against intruding birds. In great tits, the bird stretches itself up and displays the striking black and yellow underparts (Perrins 1979). In black-capped chickadees (*Parus atricapillus*) such displays are given during agonistic

situations when two confronting birds give warning calls, stretch the heads up and display a series of movements towards each other (Popp *et al.* 1990). In this species the occurrence of such displays indicate the winner of the confrontation. Dominant individuals are likely to win and they always face directly towards opponents during the displays, whereas the losers tend to face away from their opponents (Popp *et al.* 1990). Such behaviour may well occur in coal tits but, as with many aspects of the vocal repertoire and other behaviour of this species, it remains unexplored.

OUTLINE OF THE THESIS.

From previous sections, it appears that there are many factors involved in the shaping of bird songs. Those factors may not only work at the species level, but also at the population level so that different populations of a species may show differences in song structures. Chapter 2 evaluates and compares the variability of song structures in two coal tit populations, and describes more general aspects of coal tit songs.

Within a population the process of song acquisition may influence the distribution of songs. To understand this process, the study reported in this thesis has looked at the song distribution within coal tit populations, and at the effect of distance between individuals on the composition of their repertoires. The results are presented in Chapter 3 which discusses the findings with regard to the process of song distribution.

As mentioned in previous sections, songs function in mate attraction and territory maintenance. Earlier, the possible correlation between a male's quality and the songs he performs has also been mentioned. There has been a suggestion that singing performance is affected by exhaustion in the neuro-muscular coordination involved in sound production, and that declining singing performance due to such exhaustion may be recovered by switching between types of songs during singing activity (Lambrechts & Dhondt 1988). In order for a bird to be able to switch song types he must have a repertoire of songs, and this idea may thus explain why most passerine birds have repertoires. This idea was tested on coal tits, and the findings are reported in Chapter 4.

Some authors (e.g. Weary *et al.* 1988, 1991) have tried to test the anti-exhaustion hypothesis mentioned above, but found mixed results. The question was : do birds perceive individuals singing a bout of songs with declining output as weak individuals, or those singing a song bout of increasing output as fitter individuals ? Put in another way, does a song bout give information about individual fitness ? If it does, the birds would respond in accordance with information they perceive. Earlier, the suggestion that song length may indicate male 'stength' and/or male 'quality' has been mentioned. McGregor (1988) has tested this idea on chiffchaff (*Phylloscopus collybita*), but failed to find the evidence supporting the idea. Do birds perceive individuals singing long songs as fitter individuals, and those singing shorter songs as weak ones ? Playback experiments were carried out in order to answer these questions, and the results are presented in Chapter 5.

Chapter 6 presents the summary of the findings in this study, evaluates the study and proposes ideas which might be carried out in order to enhance understanding about vocal communication in coal tits.

CHAPTER 2.

VARIABILITY OF SONG STRUCTURES IN COAL TITS

INTRODUCTION

The coal tit (*Parus ater*) has a very extensive range extending over most of the Palaearctic. Its distribution in Europe extends from Scandinavia southwards through southern Europe to northern Africa, and south-eastwards through the Balkans as far as Iran (Perrins 1979). Based on his review, Göller (1987) suggested a relation between the sound production, particularly song, with the migratory behaviour of the species. He did not, however, give any explanation of how such a relationship could affect song development in this species. Perrins (1979) points out that this species is largely sedentary, and that long-distance movement in it is related to feeding conditions. He suggests that when food availability is inadequate some birds, particularly young ones, will be forced out to search for another area where the food is available. Scherrer (1972) found that large numbers of both young and old birds in an area induced the movement of many birds. This might suggest that any movement, especially a long-distance one, in coal tits might be a result of intra-specific competition when the food is inadequate. Göller (1987) was, however, quite right in saying that there was no substantial research based on the songs of this species compared to other members of the Paridae family.

Coal tit songs are generally simple, composed of two or more elements which are repeated several times in quick succession. Despite such simplicity, this species has repertoires, i.e. an individual bird sings several versions of its songs, and may have an average of 12 different song types. Generally bird songs are reckoned to deliver the same messages although in some species, such as black-throated green

warbler, *Dendroica virens*, (Morse 1970), chestnut-sided warbler, *Dendroica pensylvanica*, (Lein 1978) and bridled titmouse, *Parus wollweberi*, (Gaddis 1983), it has been reported that different songs are used in different situations. Göller (1987) suggested that 'song-like' utterances in coal tit were used in different contexts but the utterances to which he refers could be its calls, and bird calls are generally thought to serve different functions. Catchpole (1979), for example, pointed out that calls are given in specific contexts related to changes in a bird's motivation. However, the generally acknowledged functions of songs are in mate attraction and in the repulsion of potential intruders.

If songs are to serve such functions, why do birds have repertoires ? A number of hypotheses have been proposed to explain the phenomenon (see Chapter 4 for a review). One of the hypotheses is that repertoires are an adaptation to reduce habituation in other birds (Hartshorne 1956, Falls & Krebs 1975, Krebs 1976, 1977). Whitney (1981) suggested that the effectiveness of song repertoires in reducing habituation depends on the songs in the repertoires being very different from one another.

Acoustically, songs vary in both pitch and temporal patterns. Some studies have been done to investigate the variability of songs within repertoires in these respects, but they gave mixed results. Krebs (1976), for example, found that in great tits (*Parus major*) the variability within repertoires was only significantly different from that between repertoires in one respect, i.e. the phrase length. When the songs were classified by the structure of elements within

phrases, the variability within repertoires was not different from that between repertoires. This phenomenon has not been studied in coal tits.

In this chapter, the singing behaviour of coal tits and more general aspects of coal tit songs are described in addition to the evaluation of within- and between-repertoire variability in the structures of coal tit songs. Because the repertoire size of the coal tit can range from 6 to 12 song types (see Chapter 3), it is possible that smaller repertoires show less variability than larger repertoires. The association between repertoire size and variability within repertoires was, therefore, investigated. The comparison between two populations of coal tits is also made to investigate whether two populations of coal tis were significantly different in the structures of their songs.

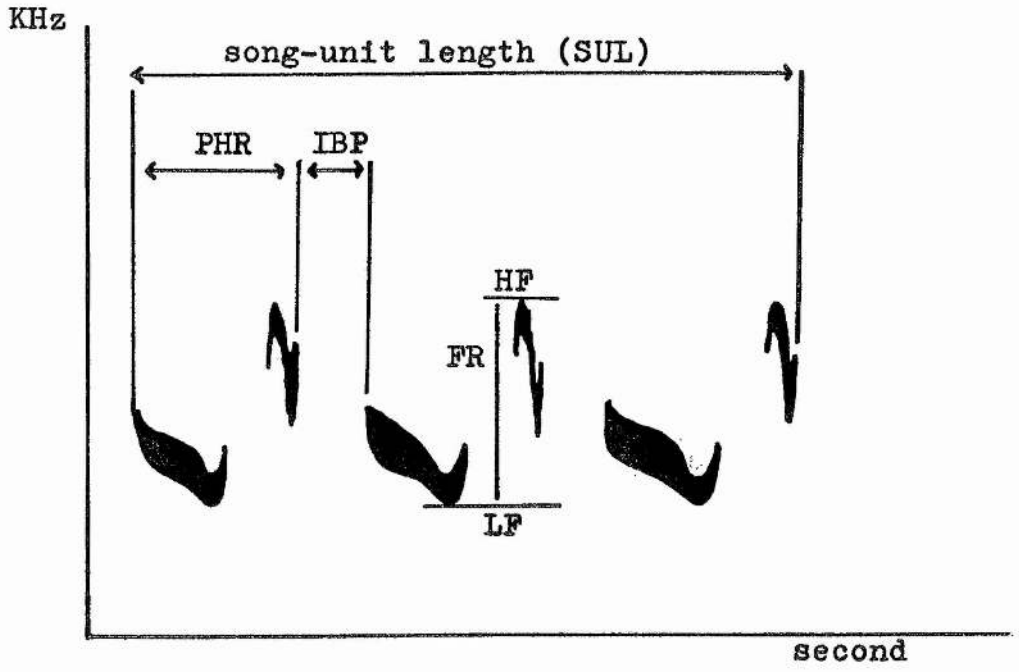
METHODS

Song recordings were made in the Tentsmuir forest and Loch Garten nature reserve. The Tentsmuir forest is a commercial coniferous forest located in North-East Fife, Scotland. The forest is homogenous and dominated by lodgepole pines (*Pinus contorta*) which are of varying ages. On the other hand, the forest in the Loch Garten nature reserve, which is located in Inverness-shire, Scotland, is a mature woodland and is more heterogenous than that at Tentsmuir; Scots pine (*Pinus sylvestris*) is the predominant tree in the forest. The recordings in Tentsmuir forest were made in 1989, 1990 and 1991. Those done in 1989 and 1991 were not so intensive and

so they were not used for assessing the repertoire size of the birds in the forest in those years. However, they could give an indication of song changes through time within the population. The recordings at Loch Garten were made in 1990 and 1991. Those in 1990 were during a short period of time so they were not used for estimating repertoire sizes. During the recording sessions at both locations, the behaviour of singing birds was observed.

Songs were analysed using the DSP Sonagraph model 5500 (Kay Elemetric Co) and sonagrams were prepared using the DSP printer model 5510. Songs with the same sonagraphic shape and acoustic characteristics were categorised as the same song types. Because the distinct song types recorded during the study were numerous, each song type was assigned a letter and a number. For example, A_1 was referred to as song type A number 1. Temporal and pitch variables were measured directly from the DSP screen/monitor since this machine provides real time analysis. The variables measured were the number of elements in a song unit (abbreviated as **NOE**), the length of song unit (**SUL** - in seconds), the length of phrases (**PHR** - in seconds), the interval between phrases (**IBP** - in seconds), the highest (**HFR**) and lowest (**LFR**) frequencies in a song unit, and the average (**AFR**) and range (**RFR**) of frequency in a song unit; the frequency measure was Hertz (Figure 2.1). In addition, the proportion of time occupied by sound production in a phrase (**SPP**) and that of time occupied by phrase production in a song unit (**PPS**) were also measured. The sound production in a phrase was referred to as the proportion of time sound was produced in a phrases. The

Figure 2.1. A song of coal tit with variables measured in the study. PHR=phrase length; IBP=interval between pauses; HF=highest frequency; LF= lowest frequency; FR=frequency range; average frequency (AF)=(HF+LF)/2; sound production in a phrase (SPP)=(total length of elements in a phrase)/PHRx100; phrase production in a song (PPS)=(total length of phrases in a song)/SUL x100.



phrase production in a song unit was the proportion of phrase produced in a song. Both are quoted in percentages. Sixty-seven types of songs, 38 from Tentsmuir and 29 from Loch Garten, were measured in all, and 20 song units of each song type were randomly chosen as samples.

RESULTS

Singing behaviour.

In general, the birds sing while searching for food, and they sing more actively when neighbouring birds also sing, especially during March when they begin to establish territories. During this period territorial disputes were frequently observed when two males sang at each other at short range. Each male always used the same singing posts both during territorial conflicts and during territorial establishment while foraging.

During territorial advertisement the birds sang a song type repeatedly for as long as 56 songs. They rarely changed song types when singing alone and moving from one tree to another, but when a neighbouring bird was also singing they usually changed song type while moving towards the spot where the neighbouring bird was. When the bird heard a singing neighbour (or an intruder) from a distance, it often would perch at the top of the canopy as if looking for the singing bird. Counter-singing with neighbouring birds did not always involve song-matching. Counter-singing sometimes induced fierce territorial confrontations, and in this situation the birds often abandoned singing in favour of a series of high

frequency calls. In the disputes, wing-spreading and wing-flickering were frequently observed as an aggressive behaviour. In playback experiments (see Chapter 5), the birds did not always respond with songs as soon as playback begun, but they often responded with such behaviour while moving towards the speakers. Warning calls were more often given when the song rate of playback was increased (see also Chapter 5).

Repertoire size.

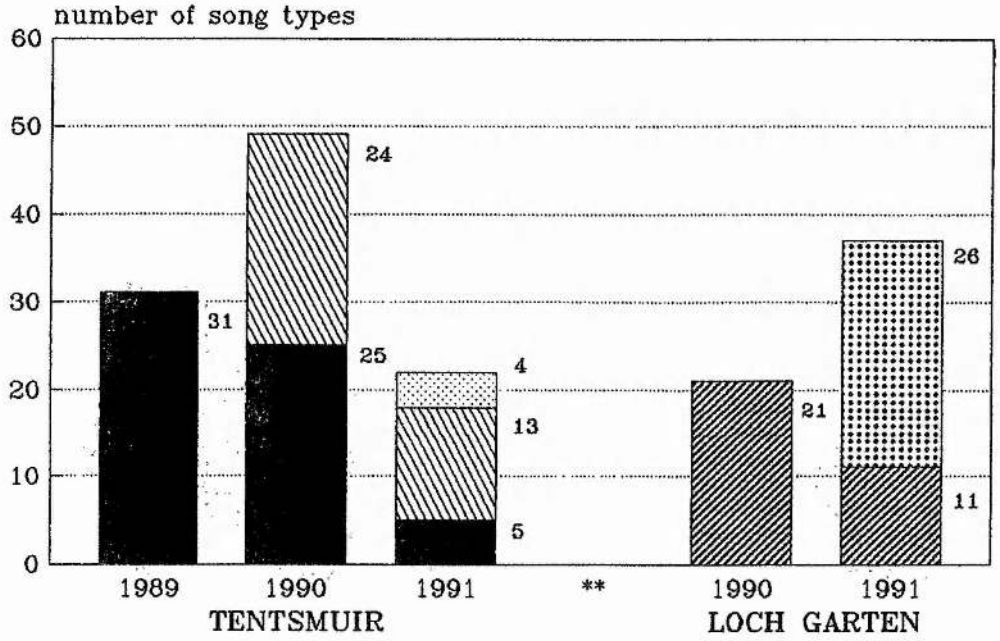
The birds in both locations sang between 6 - 19 different song types with an average of 12 song types for the Tentsmuir birds and 10 for those at Loch Garten (see Chapter 3 for more details). The estimation of repertoire size was affected by the length of recording sessions : the observed size was lower than the expected size calculated using Wildenthal's method (described in Howard 1974) when the sessions were short (see also Chapter 3 for details).

Song type changes within populations.

Fifty-nine song types were recorded at Tentsmuir and 33 at Loch Garten. Figure 2.2 shows the changes in the number of song types recorded at Tentsmuir between 1989-1991, and at Loch Garten during 1990-1991. The length of recording sessions, which was different from year to year, might have some effects on the representativeness of songs from the populations, particularly that of Tentsmuir in 1989 and 1991, and of Loch Garten in 1990.

However, by assuming that : (1) each song type within a population had the same probability of being recorded, hence

Figure 2.2. Number of song types which were recorded in a year and re-recorded in the following year.



Darkness indicates the same song types which were recorded during 1989-1991.

the song types recorded each year consituted random samples, and (2) the number of song types within a population was roughly constant from year to year, the rate of change of songs with time within a population could be tentatively estimated. The following tentative estimation will only look at the songs recorded at Tentsmuir.

The total number of song types within the Tentsmuir population was unknown, but this could be estimated using the 'capture-recapture' method which is usually used in ecology for assessing the population of a species of animal, since the structure of the available data made it possible to do this. The loss or gain of song types from year to year was estimated as the proportion of song types missing or newly recorded, respectively, compared to the number of song types within the population estimated using the capture-recapture method.

A worked example of use of the capture-recapture method is given in Appendix 2.1. Using this method it was estimated that the total number of song types within the Tentsmuir population was probably about 63. The estimated total loss and gain of song types in 1990 and 1991 are as follows :

Table 2.1. The estimated total loss and gain of song types in Tentsmuir 1990-1991. *Figures are the proportion of observed values to the estimated total song song types (=63). In brackets are the observed values. See Appendix 2.2 for details.*

	1990	1991
Total loss (%)	9.52 (6)	58.73 (37)
Total gain (%)	38.09 (24)	6.35 (4)

If the rate of loss or gain of song types was estimated from the average between the years, the rate of total loss was 34.12% and that of total gain was 22.22%. It appeared that the rate of losing song types was greater than that of gaining new song types within the Tentsmuir population. This, perhaps, indicates that song types may dissappear from the population more quickly than the introduction of new song types. However, sampling error due to the lack of uniformity of song type sampling during the study might have affected the results.

Variability within and between repertoires.

Although numerous song types were recorded in both locations, the analysis for this study was restricted to those birds which were studied intensively. These were 15 birds from Tentsmuir and 12 from Loch Garten; a total of 67 song types were used in this study. The first analysis was carried out on all birds, and the second was done on each population separately. In the analysis a one-way anova was applied using Minitab Release 7.

Table 2.2 shows the variability, or the sum of squares, between and within repertoires resulting from the one-way anova for each variable measured from both populations. Krebs (1976) also used the sum of squares from an anova as a measure of variability. The results showed that in all song parameters the variability within repertoires was greater than that between repertoires. This may mean that there is no common song characteristic within a particular bird's repertoire, at least as far as these measurements are

Table 2.2. Variability between and within repertoires of each song-variable measured in the study for all birds from two locations.

Variables	Variability: Between	Variability: Within	$F^{*)}$	p
NOE	1,624.50	57,321.12	3.31	**
SUL	160.45	1,946.89	9.61	**
IBP	0.13	1.04	14.57	**
PHR	11.03	28.45	45.24	**
SPP	5,264.80	68,248.40	9.00	**
PPS	14,824.60	104,599.80	16.53	**
HFR	798.0×10^6	$4,808.0 \times 10^6$	19.37	**
LFR	32.8×10^6	615.4×10^6	6.23	**
RFR	730.0×10^6	$5,782.0 \times 10^6$	14.74	**
AFR	495.8×10^6	$2,659.6 \times 10^6$	21.75	**

*) d.f.between = 26, d.f.within = 6093, ** = p<0.01

Table 2.3. Variability between and within repertoires of each song-variable measured in the study for the birds at Tentsmuir.

Variables	Variability: Between	Variability: Within	$F^{*)}$	p
NOE	559.560	33,491.660	2.15	**
SUL	18.050	825.570	2.82	**
IBP	0.024	0.562	5.48	**
PHR	0.717	10.281	8.99	**
SPP	3,026.800	31,455.600	12.41	**
PPS	6,222.000	51,086.000	15.70	**
HFR	35.6×10^6	918.1×10^6	5.00	**
LFR	12.3×10^6	425.5×10^6	3.72	**
RFR	51.0×10^6	$1,547.2 \times 10^6$	4.25	**
AFR	12.1×10^6	324.3×10^6	4.80	**

*) d.f.between = 14, d.f.within = 3626, ** = p<0.01

Table 2.4. Variability between and within repertoires of each song-variable measured in the study for the birds at Loch Garten.

Vari-ables	Variability: Between	Variability: Within	$F^{*)}$	p
NOE	774.28	23,829.44	3.63	**
SUL	59.14	1,121.43	5.89	**
IBP	0.03	0.48	6.15	**
PHR	1.00	18.17	6.15	**
SPP	1,869.80	36,792.80	5.67	**
PPS	1,394.00	53,513.80	2.91	**
HFR	109.0×10^6	$1{,}944.0 \times 10^6$	3.14	**
LFR	12.4×10^6	189.9×10^6	7.29	**
RFR	161.8×10^6	$2{,}118.0 \times 10^6$	4.26	**
AFR	22.0×10^6	$1{,}005.4 \times 10^6$	2.45	**

*) d.f.between = 11, d.f.within = 2648, ** = $p<0.01$

concerned, suggesting that characters are unique to each song within a repertoire.

Tables 2.3 and 2.4 show the differences in the variability between and within repertoires in each song variable for the birds in Tentsmuir and Loch Garten, respectively. The results showed that in each population the variability within repertoires was greater than that between repertoires for all song variables. This may suggest that even within a population of coal tits there is no song characteristic, at least from the measurements used in this study, common to all birds' songs.

The analysis was further extended to test whether there was a significant association between the size of repertoires

and the variability within repertoires. The indicator of variability within a repertoire used in this analysis was the coefficient of variation since this is a measure of variability within samples (Sokal & Rohlf, 1981). The size of repertoires in this analysis ranged from 6 to 19 song types. Spearman's rank correlation coefficient was computed using Minitab, and the results are shown in Table 2.5 as follows :

Table 2.5. Spearman's rank correlation coefficients between repertoire size and the coefficient of variation of song variables. (RS=repertoire size; n.s. = not significant)

Correlation between	r (N=27)	
RS - NOE	0.330	n.s.
RS - SUL	0.053	n.s.
RS - IBP	0.437	n.s.
RS - PHR	-0.142	n.s.
RS - SPP	-0.238	n.s.
RS - PPS	-0.001	n.s.
RS - HFR	0.349	n.s.
RS - LFR	0.395	n.s.
RS - RFR	-0.280	n.s.
RS - AFR	-0.176	n.s.

The results did not show any association between repertoire size and the variability within repertoires, as measured by the coefficient of variation. This suggests that coal tit with smaller repertoires still maintain the variability of song characteristics, at least in terms of those variables measured in this study, within their repertoires.

Variation between individuals.

The previous section dealt with the variability of song characteristics within repertoires. In this section the differences between the two populations of coal tits in song characteristics will be investigated. In the analysis the value of each variable for an individual was taken as the average value computed from its repertoire. The Student's t-test was applied using the Minitab to test differences in song variables between the population at Tentsmuir and that at Loch Garten. The results are shown in Table 2.6.

The results showed that there were significant differences between the two populations in all song variables except the proportion of sound in a phrase. The birds at Tentsmuir sang more elements in their songs than those at Loch Garten. The length of song unit, phrase and interval between phrases of Tentsmuir birds were significantly shorter than those of Loch Garten birds, but the Tentsmuir birds sang at significantly higher pitch (i.e. HFR, LFR, RFR and AFR in Table 2.6) than the birds at Loch Garten.

DISCUSSION

The main results in this study can be summarized as follows. Using ten characteristics of song, namely the number of elements in a song, song length, phrase length, interval between phrases, highest and lowest frequencies, and the range and average frequencies, coal tit songs showed a greater variability within repertoires than that between repertoires in all song characteristics. The within repertoire variablity

Table 2.6. Differences between the coal tit population at Tentmuir and that at Loch Garten. (N=number of individuals; *=p<0.05, **=p<0.01; ns=not significant).

Vari-able	Tentsmuir (N=15) mean	Tentsmuir (N=15) sd	Loch Garten (N=12) mean	Loch Garten (N=12) sd	t	p
NOE	8.570	0.431	8.085	0.604	2.35	*
SUL	1.526	0.081	1.759	0.165	4.31	**
PHR	0.294	0.015	0.372	0.021	10.93	**
IBP	0.083	0.003	0.090	0.003	5.93	**
SPP	81.14	1.19	81.48	0.950	0.84	ns
PPS	66.48	1.59	68.51	0.830	4.26	**
HFR	8470.0	105.0	7790.0	233.0	9.38	**
LFR	3351.2	58.9	3250.1	73.1	3.14	**
RFR	5141.0	123.0	4541.0	277.0	6.99	**
AFR	5920.1	61.5	5528.0	107.0	11.32	**

was also greater than that between repertoires when examined separately for the two populations of coal tits. There was no indication of correlation between repertoire size and the variability within repertoires. The differences in song parameters between two populations of coal tits were also significant. The coal tits at Tentsmuir sang significantly more elements in their songs, were shorter in the length of songs, of phrases and of the intervals between phrases, but sang at higher pitch, i.e. showed higher values of the highest and lowest frequencies, higher average frequency, and wider range of frequency, than those at Loch Garten.

The habituation hypothesis (Krebs 1976) predicts that repertoires are important in preventing other birds, whether they are potential mates or intruders, from habituating. The

results tend to support this hypothesis. Both the pitch and temporal features of coal tit songs within repertoires are more variable than those between repertoires. This suggests that each song type within repertoires may have distinct characters. This might enhance the effectiveness of repertoires in countering habituation (Krebs 1976). In great tits (*Parus major*), Krebs (1976) found a greater variability of phrase length within repertoires than that between repertoires. Whitney (1981) found that the dominant frequency and period of modulation were more variable within the repertoires than between those of varied thrushes (*Zoothera naevia*). In the songs of red-winged blackbirds (*Agelaius phoeniceus*), however, Yasukawa (1981) did not find any significant difference between the variability within repertoires and that between repertoires of four song characters : song length, number of introductory notes, trill modulation, and frequency of the longest introductory notes.

Krebs (1976) suggested that his results might be simply due to song sharing between birds within a population with a small number of song types. Kroodsma (1982) suggested that song learning (i.e. imitation) may lead to song-sharing among individuals within a population and result in a convergence in song characters within the population. Whitney (1990) rebutted Kroodsma's (1982) argument that such convergence may only occur in an extreme situation, such as in species which are disposed to learn a single version of each song type present in a population, or when birds learn songs primarily from a single tutor. He took Bewick's wrens, *Thryomanes bewickii*, as an example of species in the first situation, and zebra finches, *Taeniopygia guttata*, in the latter. He

reckoned that neither great tit nor varied thrush is amongst species of these types. He then suggested that sample size might be a problem with the analysis of song similarity within repertoires. He found that biases in the results were linked to both sample size of songs and of birds, whereby an increase in sample size would decrease the magnitude of the bias. He also suggested that song structures may vary micro-geographically, and that the variability within repertoires would be obviously expected in the species that show microgeographic variation.

Considering these arguments, the results in this study can be evaluated in terms of both sample size and microgeographic variation. The analyses in this study should not be affected by the sample size problem. There were 27 birds with a total of 67 song types, and 20 song units were randomly chosen as samples of each song type for the analyses. There was a possible influence of geographic variation since the birds were from two different populations. However, when each population was analysed separately - one population was of 15 birds with 38 song types, and the other was of 12 birds with 29 song types - the results still showed a greater variability within repertoires than between repertoires in all song characteristics measured in this study for each population.

There is also a possibility that microgeographic variation within each of the two coal tit populations might influence the results. As revealed in Chapter 3 the degree of song sharing between individuals was significantly related to distances between them, suggesting that there were distance

effects on song acquisition when songs were acquired through learning.

Krebs & Kroodsma (1982) have suggested that the accuracy of song learning, among other factors, plays an important role in the variation of songs on a microgeographical scale. They also indicated that individual improvisation may play a greater role than song imitation when the songs of neighbouring birds show differences. Thielcke (1973) suggested that coal tits are able to improvise the songs that they learn. Song improvisation may lead to variability within repertoires and this may eventually enhance the effectiveness of repertoires for preventing other birds from habituation.

Kroodsma (1982) suggested a convergence of song characters within a population when song learning leads to song sharing between individuals within the population. Whitney (1990) argued that such convergence might only occur in extreme cases as mentioned earlier. Such a convergence also seems unlikely to occur in species that improvise the songs they learn or do not copy accurately. Young coal tits are reported to be able to innovate new songs (Thielcke 1973), although it is unclear whether such innovation is an active process due to the coal tit's ability *per se* or stems from the inaccuracy of song imitation.

The results showing differences in song characteristics between two populations of coal tits may not be a surprise. Krebs & Kroodsma (1982) suggested that vocal variation between populations may occur when they are isolated from each other. The two populations in this study were separated from each other by a considerable distance, and this species is largely sedentary (Perrins 1979), so that it is likely that they are

isolated from each other. There is little possibility that cultural transmission occurs between the two populations and their songs are likely to develop independently from each other. However, the exact nature of the differences between these populations may be related to ecological factors, or in other words, to habitat adaptation.

In the evolution of avian vocalizations the acoustic characteristics of the habitat are thought to play an important role (Morton 1975). Factors such as differences of sound propagation or attenuation in different habitats (e.g. Morton 1975, Marten & Marler 1977, Marten *et al.* 1977, Wiley & Richards 1978, Hunter & Krebs 1979) or the total sound environment produced by local avifauna (Brown 1977) act as selective pressures in shaping avian vocal characteristics. It has been suggested that songs with higher frequency are associated with a field environment, and those with lower frequency with forested environments (Wasserman 1979). How far the songs will be transmitted is determined by many factors that accelerate sound propagation or attenuate the sound. The density of trees as well as foliage density and ground vegetation within a habitat determine the degree of sound attenuation, and climatological factors such as wind, temperature or humidity also affect sound propagation (Morton 1975, Marten & Marler 1977, Marten *et al.* 1977). To some extent, territory size and perch height where the birds sing influence song propagation (Marten & Marler 1977, Hunter & Krebs 1979). In great tits, however, Hunter & Krebs (1979) did not find an effect of perch height.

The explanation of why the two coal tit populations showed significant differences in their song structure is more

speculative. Tentsmuir and Loch Garten are similar in their habitat characteristics, in that they are coniferous woods. The obvious difference is that tree density in Tentsmuir is higher than that at Loch Garten, and the ground cover at Loch Garten is taller with more variety of vegetation than at Tentsmuir (Williams 1991). If Loch Garten were categorized as more 'open' than Tentsmuir, the birds at Loch Garten might be expected to show higher pitch characteristics in their songs. The results did not suggest that this was the case. If it were to be assumed that the ground effect, which will attenuate the songs, was higher at Loch Garten than at Tentsmuir because the ground cover was more dense in Loch Garten, the birds would again be predicted to sing at higher frequencies, and yet this was not the case.

The possible factors that made the two populations different in their song characteristics are the total sound environment, as influenced by climatological factors or local avifauna, and the size of territories. Territory size was difficult to assess since the birds were not ringed, but using their prominent singing posts as territory boundaries, and assuming that the same birds used the same singing posts, territory size within sites seems to vary considerably. The territory size between the two populations may be different, but this would need further evidence.

No attempt was made to investigate the density of avifauna in the two locations, but Loch Garten appeared to have more species than Tentsmuir. Whether this would make the song development in the two populations different is unclear. However, it has been suggested that there is a tendency for different species living in the same area to avoid temporal

overlap (Cody & Brown 1969), and this may make it unnecessary for birds to sing louder than others.

Wiley & Richards (1978) suggested that climatological factors such as wind and temperature gradients in more open habitat have strong effects on sound propagation by which higher frequencies are scattered. From casual observation it seems possible that the wind and other sources of habitat noise may be a reason for the differences between the two populations. The noise from wind, sea-noise or aircraft seems higher at Tentsmuir than at Loch Garten. Perhaps because Tentsmuir is located by the coast it is exposed to strong wind from the sea blowing through the wood and creating a noisier environment, in addition to sea-noise itself and aircraft, as it is near an RAF base. If this was the case the birds in Tentsmuir would be expected to sing at higher pitch as a counter to high levels of low frequency noise. This, however, needs more clarification.

That the birds in Tentsmuir sang with shorter temporal features in their songs (i.e. shorter song length, phrase length and interval between phrases within a song unit), might be caused by the increase in their song frequencies. Presumably, singing at higher pitch is more energy-consuming which may cause the birds to become easily exhausted. The birds may avoid such exhaustion by singing shorter songs or phrases. But maybe there are still other factors which could explain this better, and there is undoubtedly need for more information.

CONCLUSION

The main results in this study can be summarized in terms of the habituation hypothesis and that of habitat acoustic adaptation. The results support the habituation hypothesis, which proposes that repertoires are important in countering habituation in other birds, potential mates or potential intruders. There was no significant association between repertoire size and the variability within repertoires.

The song structures of two coal tit populations from different locations differed significantly in both temporal and pitch characteristics. Both populations develop their songs independently from each other. A possible factor which may have led to such differences was habitat acoustics, where in a habitat with a noisier environment due to wind, sea-noise and other sources of noise, coal tits had to increase their pitch to transmit their songs effectively. But, if singing at higher pitch is exhausting, then this could explain why the birds at Tentsmuir sing songs with shorter temporal characteristics. All this, however, is still speculative, and more information is needed for clarification of the various issues involved.

CHAPTER 3.

SONG DISTRIBUTION WITHIN POPULATIONS

INTRODUCTION

Most *Parus* species (Paridae) sing relatively simple songs and in this the male coal tit (*Parus ater*) is no exception. Coal tit songs consist of phrases of two to five elements which are repeated for as long as five to eight seconds (Latimer 1977, Göller 1987). An individual male can possess a repertoire of 12-16 different song types (Göller 1987). It is common in species with repertoires for neighbouring birds to copy each other's song types (Krebs & Kroodsma 1982). Such a learning mechanism, if it is accurate, leads to some song types being widespread within a population. That mechanism can also bring new song types into the population when transcription errors occur (Slater & Ince 1979). New song types may also appear as a result of their introduction by individuals into the population after they were learnt somewhere else (Slater & Ince 1979).

Song type copying in a population of chaffinches occurred at random (Slater *et al.* 1980) suggesting that all song types within a population were equally likely to be learnt by individuals once allowance was made for differences in abundance. The distribution of song types in a population is likely to be influenced by both repertoire size and the number of neighbours (Williams & Slater 1990). A male with fewer neighbours might be exposed to a smaller number of song types which could be copied than one with more neighbours. The number available for copying, however, depends on the size of repertoires as well as the number of neighbouring birds.

From their simulation study, based on chaffinches, Williams & Slater (1990) found that the number of neighbours affected the number of birds that shared the commonest song.

It is then likely that the occurrence of common songs within a population depends on the degree of song sharing between neighbouring birds. McGregor & Krebs (1982) showed, however, that there was no tendency for the songs within a great tit population to be commoner or rarer than expected by chance. They also found that song sharing was negatively correlated with distance, i.e. birds that were further separated shared fewer song types.

Several hypotheses have been put forward to explain the significance of song sharing. Song sharing may : (1) allow birds to recognize neighbours (Searcy *et al.* 1981); (2) allow birds to match neighbours' songs in counter-singing duels (Krebs *et al.* 1981); (3) act as a means of signalling distance (Falls *et al.* 1982, Shy & Morton 1986); and (4) enhance breeding success by having better mating, nesting and fledging success (Payne 1982, 1983). Although this study does not attempt to test these hypotheses, it looks at the degree of song sharing between individuals within coal tit populations, and discusses it in relation to these hypotheses and to song development. In addition to that, this study investigates the distribution of song types within the populations as well as the size, composition and distribution of repertoires within the populations.

METHODS

Study sites.-- This study is based on recordings from two discrete populations of coal tits. The first population

was found in Tentsmuir forest which is a commercial coniferous forest located in North-East Fife, Scotland. The forest is dominated by lodgepole pines (*Pinus contorta*) and is managed such that different parts of the forest contain trees of varying ages. There were more than 30 male coal tits in the forest, and 15 of these were subjected to intensive recording sessions in February-June 1990 in order to collect detailed recordings and observations. These males were a small population living in the north-eastern area of the forest which covers approximately 2.1 km^2. For the same purpose 12 males, which constituted a small population in the Loch Garten nature reserve, Inverness-shire, Scotland, were recorded in May 1991. The Loch Garten nature reserve is within a vast area of ancient Scots pines (*Pinus sylvestris*).

In each population the territories were mapped using the singing posts which were regularly used by each territorial male during its singing activity, assuming that the same birds used the same singing posts as territory boundaries. Neighbours which used their respective singing posts for counter-singing also made it easier to map their territories. Recordings in both places were made using a Marantz CP430 tape-recorder. In Tentsmuir forest the recordings were made with a Sennheiser MD400 microphone mounted in a 50 cm diameter parabolic reflector, whereas at Loch Garten a Sennheiser MZW 816 gun-microphone was used. Songs from each male were analysed using a DSP Sonagraph model 5500 (Kay Elemetric Co.) and sonagrams were prepared using the DSP Printer model 5510. Songs with the same sonagraphic shape and acoustic characteristics were categorised as the same song type. Each

song type was assigned a letter and a number for identification (see Chapter 2).

Sampling of repertoires.-- Each male of the Tentsmuir population was subjected to an average of 39 recording-hours. Because the length of recording sessions in each recording-day was not always the same for each bird, the sessions were clumped into recording-hours against which new song types recorded were plotted (see Figures 3.1 and 3.2). When no more new song types were recorded, the accumulative new song types reached an asymptote, and this was used as an estimate of observed repertoire size. The same method was applied to the birds at Loch Garten. Each male in this study area was subjected to an average of 7.5 recording-hours. Here, new song types recorded were plotted against recording-sessions with 0.5 hour intervals.

In estimating the repertoire size of the mockingbird (*Mimus polyglottos*), Howard (1974), using the method described by Wildenthal (see Howard's reference), plotted the number of distinct syllable patterns as a function of the number of syllable patterns in a sample to obtain a curve that showed the probable limit of a bird's repertoire. This was reached when the rate of introduction of new syllables reached its asymptote. The repertoire size was then estimated using the following equation :

$$n = N\ (1 - e^{-T/N})$$

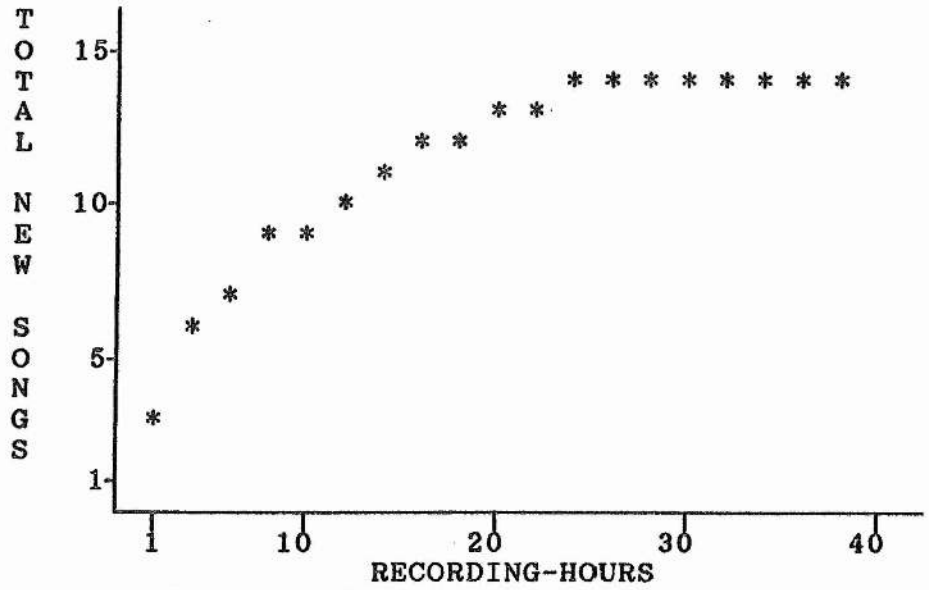
where n is the number of distinct syllables found in the sample, T is the total number of syllables recorded, and N is

the total number of syllables in the repertoire. Using this method, the results showed similar patterns to the one used in this study (see Figures 3.1.b and 3.2.b). With this method, N is the estimated repertoire size, n is the number of song types recorded, and T is the total number of song types recorded during all the recording sessions for a particular bird. Tables 3.1 and 3.2 show the estimated and observed repertoire of birds in the two populations. When they were treated with the Chi-square test, there was no significant difference between the expected and observed repertoire sizes in the Tentsmuir population (X^2=6.5, df=14, N.S.), but there was significant difference between them in the Loch Garten population (X^2=21.61, df=11, $p<0.05$). This might have been the result of shorter recording-sessions which underestimated the repertoire size of the Loch Garten birds.

Analysis of song structures.-- The similarity of song types based on their song structures was investigated, and a question was put forward whether similar song types would occur in the same repertoires. For this, ten song characters were measured from each song type. As in Chapter 2, song characters were directly measured from the DSP monitor, and a total of 67 song types from 27 birds were studied from each of which 20 song units were taken as samples. The song characters were the number of elements in a song, song length, phrase length, interval between phrases, proportion of sound production in a song and in a phrase, the highest and lowest frequencies in a song, frequency range and average frequency (see Chapter 2 for details).

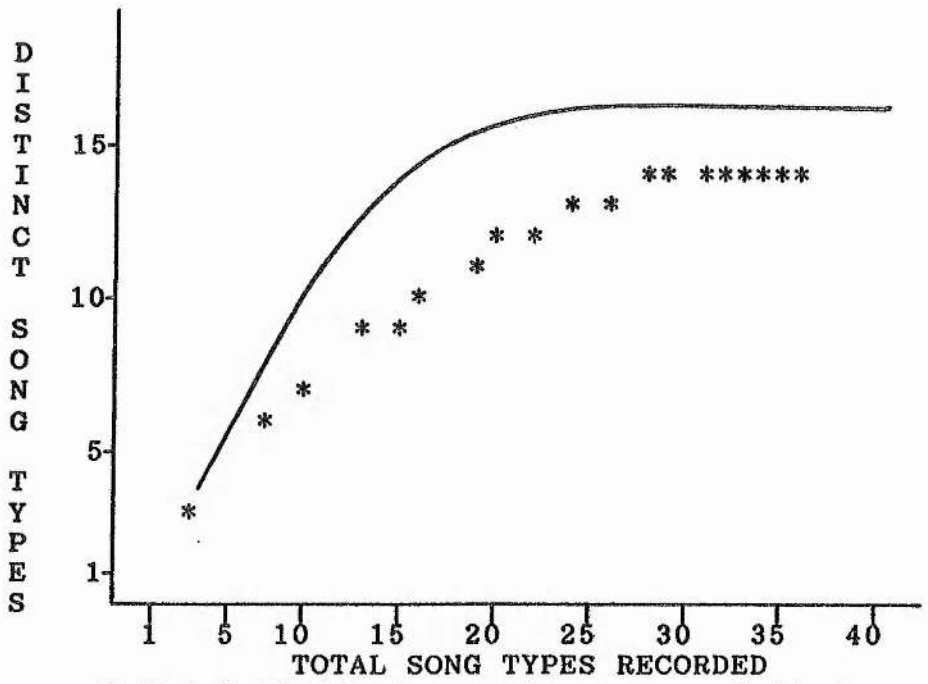
Figure 3.1. Total new song types recorded in Tenstmuir as a function of : (a) recording hours, and (b) total song types registered.

a. Bird 1



* *The accumulative new song types recorded each recording-day.*

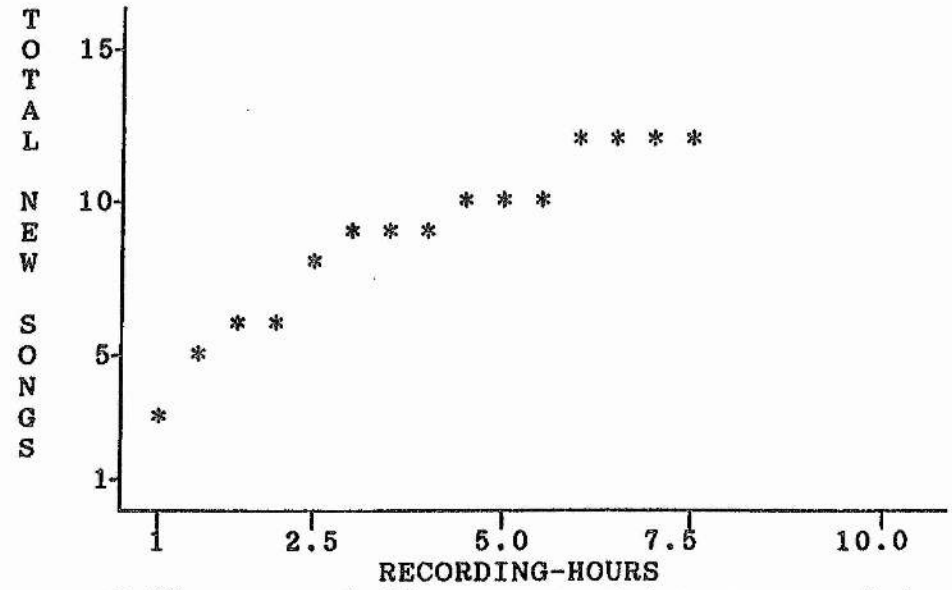
b. Bird 1



* *Total distinct song types are plotted as a function of total song types recorded.*
\- *Curve represents the expected distinct song types, calculated using Howard's (1984) exponential equation* - see Text.

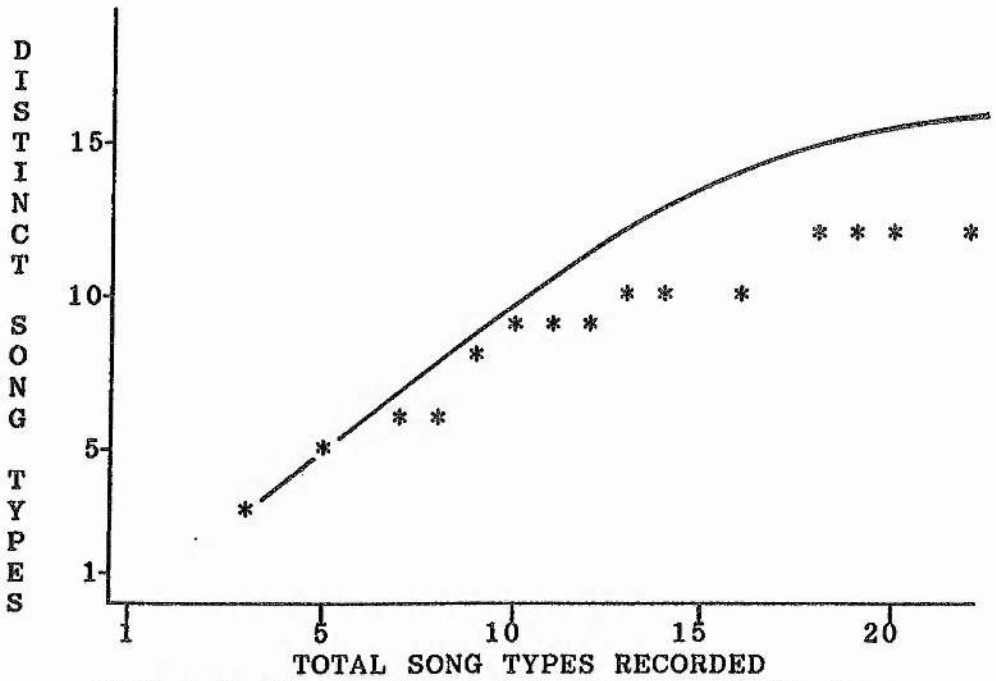
Figure 3.2. Total new song types recorded in Loch Garten as a function of : (a) recording hours, and (b) total song types registered.

a. Bird 2



* *The accumulative new song types recorded each recording-day.*

b. Bird 2



* *Total distinct song types are plotted as a function of total song types recorded.*
\- *Curve represents the expected distinct song types, calculated using Howard's (1984) exponential equation* - see Text).

Table 3.1. The observed repertoire size and the expected size calculated using Howard's (1974) method for each bird in the Tentsmuir population.

Birds	Repertoire Size		X^2
	Observed	Expected	
1	14	16	0.25
2	12	14	0.29
3	11	12	0.08
4	12	15	0.60
5	16	19	0.47
6	19	24	1.04
7	11	13	0.31
8	8	10	0.40
9	13	14	0.07
10	7	10	0.90
11	16	19	0.47
12	12	13	0.08
13	14	16	0.25
14	12	14	0.29
15	6	9	1.00

X^2 = 6.50
df = 14
n.s.

Table 3.2. The observed repertoire size and the expected size calculated using Howard's (1974) method for each bird in the Loch Garten population.

Birds	Repertoire Size		X^2
	Observed	Expected	
1	15	20	1.25
2	12	16	1.00
3	11	15	1.07
4	9	14	1.79
5	10	15	1.67
6	8	14	2.57
7	10	16	2.25
8	7	14	3.50
9	11	16	1.56
10	9	13	1.23
11	14	20	1.80
12	8	13	1.92

X^2 = 21.61
df = 11
$p < 0.05$

From the 20 song unit samples per song type, the average values for each song character from all song types were used for computing the similarity between songs. The similarity measure was the coefficient of product moment correlation computed using standardized values because song characters were of different units. The standardized value was the deviation of original value from the mean divided by its standard deviation (Sokal & Sneath 1963).

The similarity coefficients between song types were then subjected to the average linkage cluster analysis (using a shareware program called MVSP; programmer : Warren L. Kovach, University of Indiana, Bloomington, USA; distribution : Shareware Marketing, England, UK). This analysis produced a dendrogram showing the groupings of song types. Using this dendrogram an investigation was done to evaluate whether similar song types were in the same repertoires. In addition, the dendrogram could also indicate whether song types from two coal tit populations were grouped into separate clusters.

Analysis of song sharing.-- Song sharing between individuals was taken as the mean percentage of the song repertoires shared between them. For example, if male A shares 60% of its repertoire with male B and male B shares 40% of its song types with male A, they then share an average of 50%. This value was then called song sharing index between males A and B. In order to investigate whether the degree of song sharing between individuals was associated with the distance between them, a linear regression analysis was carried out on song sharing indices and distances between birds. The percentage of song sharing was arc-sin tranformed

as is needed to convert percentages to a normal distribution. Since the distances between birds were not directly measured, they were estimated from the map using approximately the centre of territory as the points of comparison. The regression analysis could indicate whether distance affected the degree of song sharing. In order to investigate whether neighbouring birds were grouped within the same clusters based on their song sharing indices, an average cluster analysis was employed on the indices of song sharing between birds.

RESULTS

The total number of song types recorded from the Tentsmuir population was 38, while that from the Loch Garten population was 29. The average size of repertoire was 12.2 for the Tentsmuir population, and 10.3 song types for the Loch Garten one. Although the repertoire size of the birds in the Loch Garten area has clearly been underestimated, as the same recording-hours were devoted to each bird this should have given the same chance for each song type in the repertoires to be recorded.

Song types and repertoires in populations.

There was considerable variation in the number of birds that sang any particular song type in both the Tentsmuir and Loch Garten populations. That in the Tentsmuir population, where it ranged from 1 to 11 birds per song type (see Figure 3.3), was greater than that in the Loch Garten population. There was no significant difference between the two

populations in the number of birds that sang any song type ($t=0.96$, $df=64$, $p=0.34$). If some song types were preferred by individuals within the population more than others, the number of birds singing any song type would not be distributed at random. This was investigated by testing the frequency distribution of the number of birds per song type against a Poisson distribution.

The values for the expected frequency distribution were obtained by multiplying the probability density functions of Poisson distribution by the number of samples for each class of intervals using Minitab Release 7. Figure 3.4 shows the comparison between the expected and observed frequency distributions for both populations. The goodness-of-fit of these distributions was tested with the Kolmogorov-Smirnov test using NPAR TESTS K-S in SPSS/PC+, and the results showed no difference between the observed and the expected values from the Poisson distribution in the two populations (test-values are shown in Figure 3.4). This suggests that no particular song type was preferred to the others more than expected by chance.

Although the repertoire size of birds in the Loch Garten population was underestimated, it did not show a significant difference from that in the Tentsmuir population ($t=1.64$, $df=24$, $p=0.11$). The range of repertoire sizes found in the two populations was very similar (see Figure 3.5). If some birds preferred to have more song types in their repertoires than the others, the distribution of repertoire sizes would not be random. This was tested using the same method as for the number of birds per song type above. The comparison between the observed and expected frequency distributions of

repertoire sizes is shown in Figure 3.6. The Kolmogorov-Smirnov goodness-of-fit test was applied to investigate whether the observed distribution of repertoire size was different from the Poisson distribution. The results showed no difference between the observed and expected values in both populations (see Figure 3.6). This also suggests that the repertoire size occurred at random.

It is possible that certain combinations of song types are preferred for copying. In order to find out whether any combinations of any song types occurred within the repertoires more than expected by chance, the observed and expected values of each possible combination of song types in the two populations were computed. The observed value of any combination was the number of times that particular combination occurred within the repertoires. The expected value was computed using the following equation :

$$EXP_{AB} = R_A \times R_B / R_{AB}$$

where EXP_{AB} is the expected value of combination of song types A and B, R_A (R_B) is the number of repertoires in which song type A (B) occurred, and R_{AB} is the total number of repertoires in which A and/or B occurred. Table 3.3 shows the computation of these values.

The observed and expected values of each possible combination of 38 song types in the Tentsmuir population were computed, and so were those of 29 song types in the Loch Garten population. In both populations there were too many expected values smaller than 5.0 so that the Chi-square test

Table 3.3. An example of computing the observed and expected values of a combination of two song types. (*x = present - = absent*)

	Birds						
	1	2	3	4	5	6	Total
Song A	x	x	x	-	-	x	4
Song B	x	x	-	x	x	x	5

- Number of repertoires where A and B occurred together = the observed value = 3
- Number of total repertoires where A and B occurred = R_{AB} = 6
- Expected value = 4x5/6 = 3.33

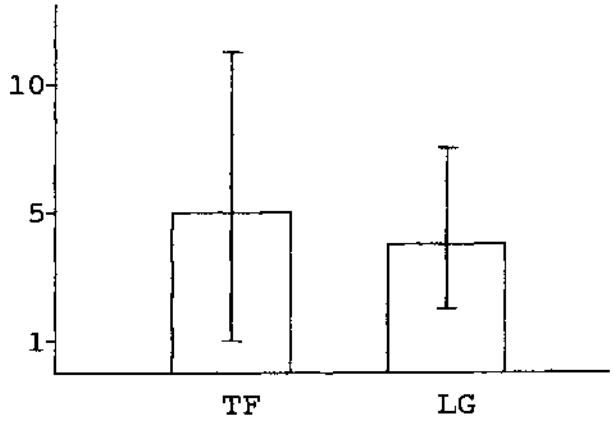
was impossible to apply. However, there were 36 song type combinations in the Tentsmuir population with the expected values greater than 5.0, and 11 song type combinations in the Loch Garten population.

Table 3.4 shows the values of both the observed and expected combinations in the Tentsmuir population, and Table 3.5 shows those in the Loch Garten population. By applying the Chi-square test on those values, the results showed no significant difference between the expected and observed values in both populations. This suggests that there was no particular combination of song types, at least from the combinations of those song types listed in Tables 3.4 and 3.5, that was preferred by the birds in the two populations.

Similar songs within repertoires.

Figure 3.7 shows the dendrogram of song type groupings based on the similarity of song structures between song types. From this figure it is clear that more than half of the song types from Loch Garten (18 out of 29) were grouped together in

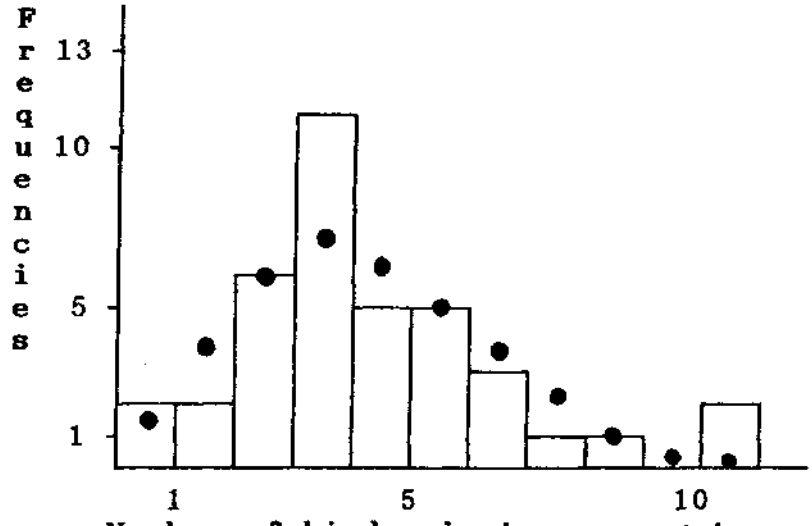
Figure 3.3. Mean number of birds singing a song type with its range in the Tentsmuir and Loch Garten populations.



TF = Tentsmuir population; mean=4.82, sd=2.24, N=38
LG = Loch Garten population; mean=4.28, sd=1.69, N=29

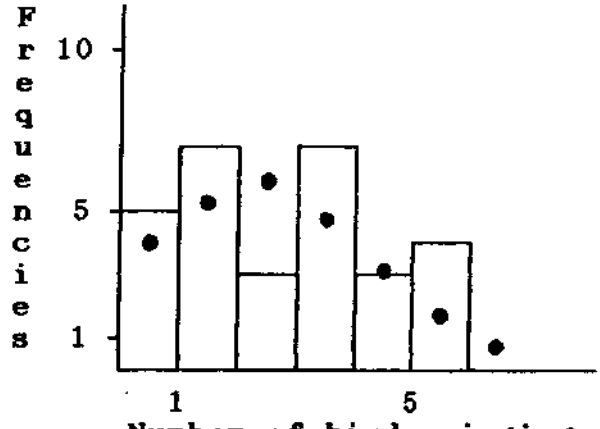
Figure 3.4. Distribution of the number of birds singing a song type in the Tentsmuir and Loch Garten populations.

a. Tentsmuir population.



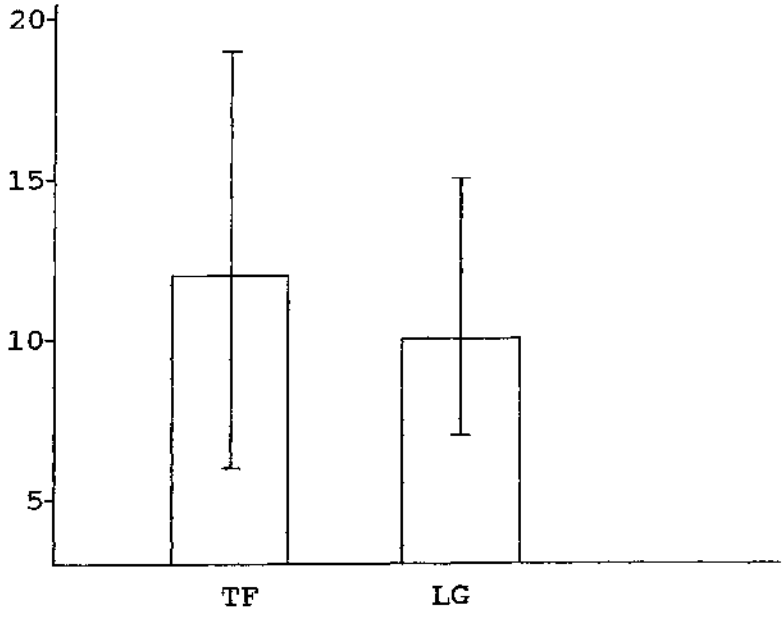
Dots represent expected frequencies based on the Poisson distribution. (D=0.09, K-S z=0.56, p=0.91)

b. Loch Garten population.



Dots represent expected frequencies based on the Poisson distribution (D=0.07, K-S z=0.37, p=0.99).

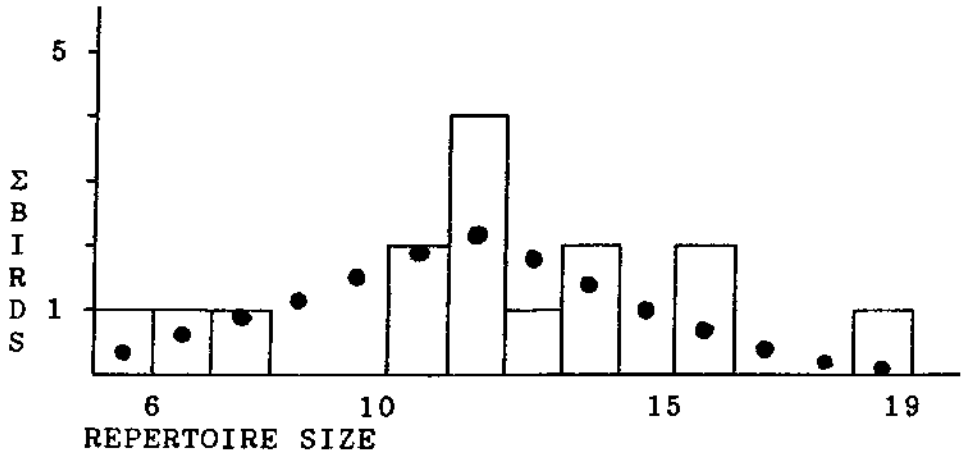
Figure 3.5. Mean repertoire size with its range in the Tentsmuir and Loch Garten populations.



TF = Tentsmuir population; mean=12.2, sd=0.90, N=15
LG = Loch Garten population; mean=10.33, sd=0.70, N=12

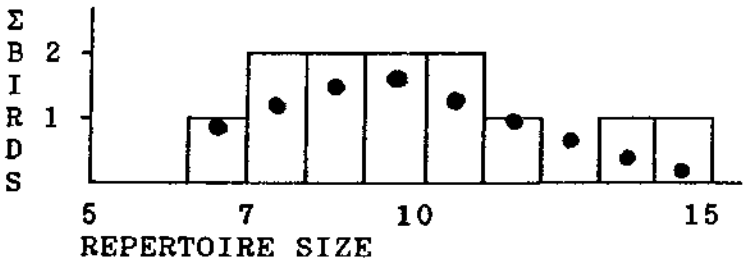
Figure 3.6. Repertoire size distribution in the Tentsmuir and Loch Garten populations.

a. Tentsmuir population.



Dots represent frequency distribution based on the Poisson distribution. (D=0.11, K-S z=0.41, p=0.99)

b. Loch Garten population.



Dots represent frequency distribution based on the Poisson distribution. (D=0.11, K-S z=0.38, p=0.99)

Table 3.4. Combination of song types with the expected values ≥ 5.00 in the Tentsmuir population.

Song type Combination	Observed Values	Expected Values	X^2
A_1B_1	5	5.25	0.012
A_1C_1	5	5.60	0.064
A_1H_1	5	5.25	0.012
A_1I_1	6	6.13	0.003
A_1M_1	6	6.13	0.003
A_1N_1	5	5.25	0.012
A_1O_1	6	6.42	0.028
A_1Q_1	4	5.50	0.409
B_1O_1	5	5.50	0.046
B_1Q_1	4	5.08	0.229
C_1H_1	5	5.33	0.020
C_1I_1	6	6.22	0.008
C_1M_1	5	5.60	0.064
C_1N_1	5	5.33	0.020
C_1O_1	5	6.29	0.265
C_1Q_1	7	7.33	0.015
C_1S_1	4	5.09	0.233
H_1I_1	6	6.00	0.000
H_1M_1	5	5.25	0.012
H_1O_1	4	5.08	0.229
H_1Q_1	4	5.08	0.229
I_1M_1	6	6.13	0.003
I_1O_1	5	5.92	0.143
I_1Q_1	5	5.92	0.143
J_1O_1	4	5.08	0.229
J_1Q_1	5	5.50	0.045
M_1O_1	5	5.92	0.143
M_1Q_1	4	5.50	0.409
N_1O_1	6	6.00	0.000
N_1Q_1	4	5.08	0.229
O_1P_1	5	5.00	0.000
O_1Q_1	7	8.07	0.142
O_1S_1	6	6.42	0.028
O_1A_1	5	5.50	0.045
Q_1S_1	3	5.13	0.249
Q_1A_1	5	5.50	0.045

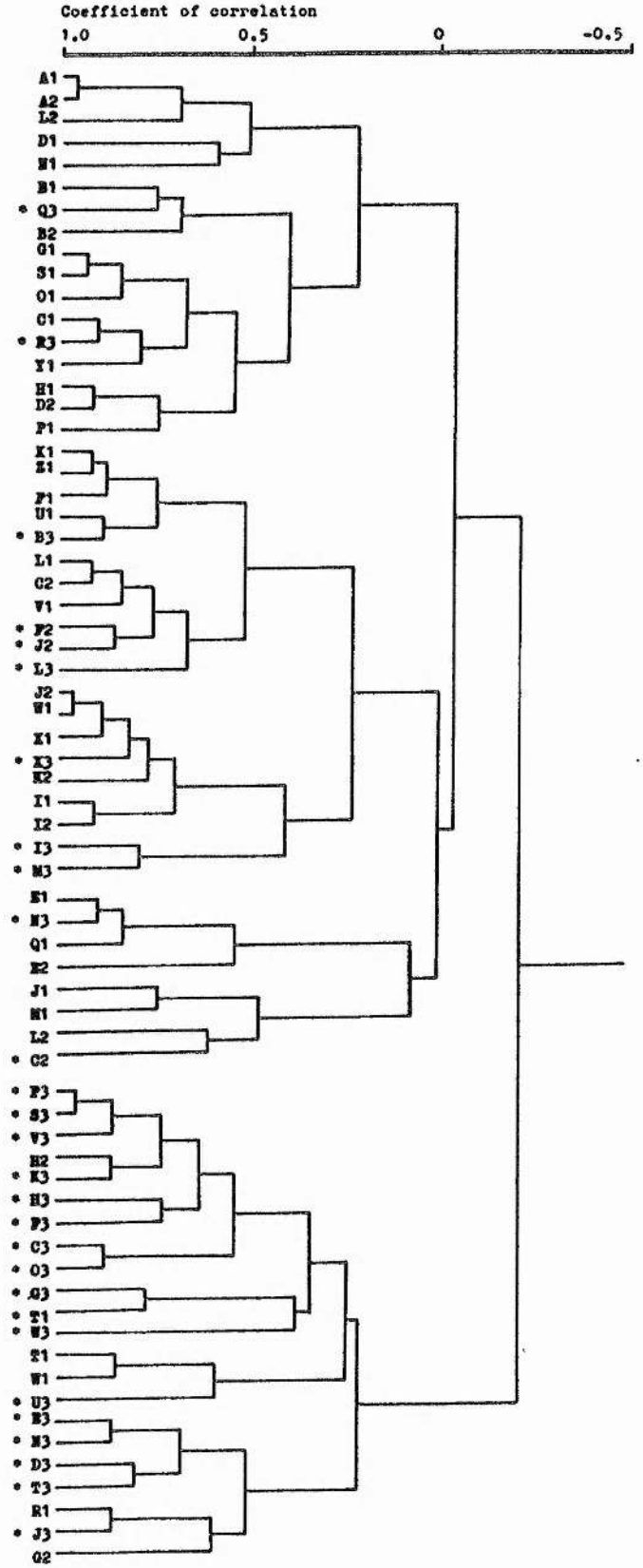
$X^2 = 3.766$
df = 35
n.s.

Table 3.5. Combination of song types with the expected values ≥ 5.00 in the Loch Garten population.

Song type Combination	Observed Values	Expected Values	X^2
E_2M_2	5	5.00	0.000
F_2K_2	5	5.25	0.012
F_2S_2	5	5.25	0.012
K_2P_2	6	6.13	0.003
K_2S_2	7	7.00	0.000
K_2V_2	5	5.44	0.036
P_2S_2	6	6.13	0.003
P_2U_2	5	5.25	0.012
P_2V_2	5	5.44	0.036
S_2V_2	5	5.44	0.036
V_2Y_2	5	5.00	0.000

X^2 = 0.15
df = 10
n.s.

Figure 3.7. Dendrogram showing the groupings of song types based on the similarity between them.



• denotes song types from Loch Garten.
Cophenetic correlation = r = 0.63
(t=38.14, df=2209, $p < 0.01$)

a cluster. This may, to some extent, indicate the occurrence of geographic variation in coal tit songs, although it is difficult to argue strongly that this is the case because not all song types from the Loch Garten population were clustered together and separated from those of the Tentsmuir population.

From two-pair clusters (i.e. the clusters of two song types) with the highest cophenetic values, there were 25 two-pair clusters each of which was expected to occur within the same repertoires. Only 12 out of these were found within the same repertoires. This simple comparison may indicate that the chance that similar song types occur within a repertoire is about the same as that they occur in different repertoires.

Song sharing and distance between individuals.

Tables 3.6 and 3.7 show the degree of song type sharing (song sharing indices) and the approximate distances between individuals in the Tentsmuir and Loch Garten populations respectively. The song sharing indices (arc-sin tranformed) are plotted as a function of the distances and shown in Figures 3.8 and 3.9. A regression analysis was employed to test whether the association between the song sharing and distance was significant for both populations.

The results showed a highly negative correlation between the amount of song sharing and the distance between individuals in both populations (Tentsmuir : $t=5.55$, $df=103$, $p<0.01$; Loch Garten : $t=6.64$, $df=64$, $p<0.01$). This suggests that the degree of song sharing between individuals decreases when they are further apart. It would then be expected that individuals with high song sharing indices would occur near to each other. In order to see whether this was the case, the

Table 3.6. Song sharing indices (upper half matrix - in %) and approximate distances (lower half matrix - in km) between birds in Tentsmuir.

	BIRDS							
	1	2	3	4	5	6	7	8
1	*	69.64	56.82	46.43	73.66	49.62	48.70	29.46
2	0.37	*	60.98	50.00	72.92	54.39	52.27	20.83
3	0.67	0.40	*	69.70	53.69	35.89	81.82	43.18
4	0.83	0.79	0.50	*	51.04	27.19	60.98	20.83
5	0.48	0.75	0.75	0.58	*	57.57	53.69	28.13
6	0.44	0.52	0.46	0.42	0.29	*	35.89	44.41
7	1.06	0.77	0.42	0.67	1.12	0.83	*	53.98
8	1.48	1.21	0.81	0.85	1.41	1.16	0.42	*
9	1.08	0.89	0.50	0.40	0.98	0.73	0.35	0.46
10	1.29	1.25	0.92	0.48	0.87	0.87	0.89	0.85
11	1.62	1.41	1.02	0.87	1.46	1.25	0.73	0.37
12	2.08	1.89	1.50	1.29	1.87	1.68	1.19	0.79
13	2.37	2.14	1.75	1.58	2.16	1.98	1.41	1.00
14	2.33	2.16	1.77	1.52	2.06	1.91	1.48	1.10
15	1.89	1.83	1.48	1.06	1.54	1.46	1.33	1.12

Table 3.6. (continued)

	BIRDS						
	9	10	11	12	13	14	15
1	23.21	10.71	48.33	7.74	21.43	15.48	11.90
2	33.33	22.62	37.50	8.33	30.95	16.67	12.50
3	43.56	23.38	39.39	17.42	16.23	17.42	12.88
4	50.00	11.31	30.00	25.00	15.48	8.33	0.00
5	51.04	20.54	38.75	21.88	26.79	21.88	11.46
6	33.99	29.32	23.86	54.39	55.83	61.18	32.89
7	52.27	11.69	31.52	26.14	8.12	8.71	0.00
8	31.25	13.39	28.75	31.25	19.64	20.83	14.58
9	*	33.93	22.50	50.00	23.21	25.00	12.50
10	0.54	*	31.43	45.24	53.57	33.93	61.90
11	0.54	0.67	*	22.50	34.52	37.50	46.67
12	1.00	0.94	0.46	*	54.17	58.33	25.00
13	1.27	1.25	0.73	0.40	*	54.17	47.62
14	1.25	1.10	0.75	0.31	0.31	*	37.50
15	1.00	0.58	0.77	0.71	0.96	0.69	*

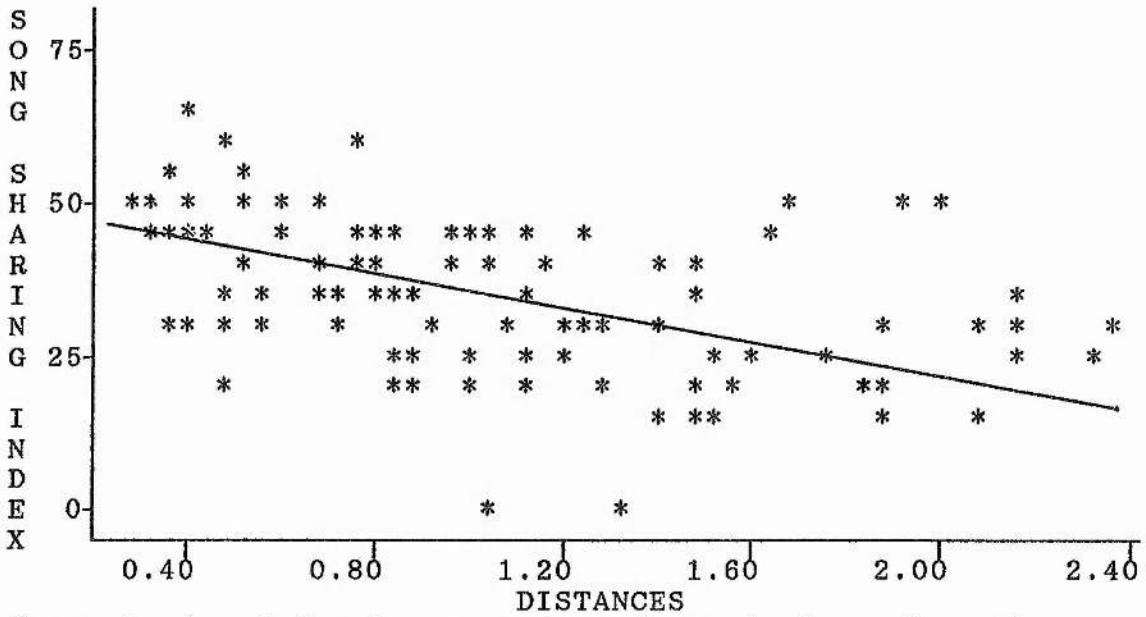
Table 3.7. Song sharing indices (upper half matrix - in %) and approximate distances (lower half matrix - in km) between birds in Loch Garten.

	BIRDS						
	1	2	3	4	5	6	7
1	*	75.00	63.03	35.56	33.33	0.00	16.67
2	0.21	*	69.70	38.89	45.83	0.00	18.33
3	0.39	0.21	*	30.30	28.64	10.80	19.09
4	2.26	2.26	2.08	*	84.44	35.42	52.78
5	1.95	1.95	1.79	0.37	*	45.00	60.00
6	1.50	1.63	1.55	1.24	0.89	*	78.75
7	1.87	2.00	1.92	1.26	0.97	0.37	*
8	2.18	2.47	2.39	1.42	1.21	0.84	0.47
9	3.02	3.10	2.97	1.05	1.21	1.66	1.39
10	3.47	3.52	3.39	1.45	1.63	2.05	1.79
11	3.13	3.24	3.10	1.42	1.47	1.66	1.34
12	3.18	3.31	3.24	1.95	1.87	1.71	1.34

Table 3.7 (continued)

	BIRDS				
	8	9	10	11	12
1	20.95	23.64	17.78	27.62	19.17
2	22.62	8.71	9.72	0.00	0.00
3	23.38	9.09	10.10	24.35	10.80
4	63.49	40.40	22.22	36.51	11.81
5	60.71	47.73	31.67	25.71	11.25
6	53.57	75.57	70.83	58.93	25.00
7	85.00	57.27	52.78	51.43	11.25
8	*	46.75	25.40	42.86	0.00
9	1.18	*	80.81	56.82	43.18
10	1.50	0.45	*	54.76	47.22
11	0.97	0.50	0.58	*	68.75
12	0.87	1.18	1.24	0.68	*

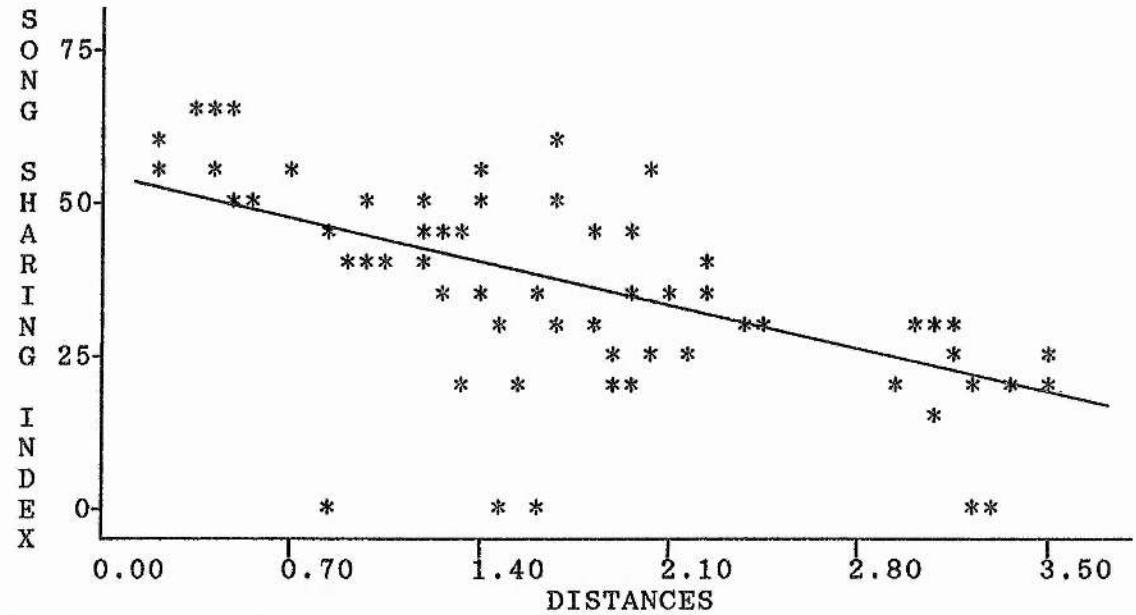
Figure 3.8. Song sharing indices as a function of distances in the Tentsmuir population.



Song sharing index in percentage (arc-sin transformed). Distances in kilometer.

Correlation of Song sharing index and Distance = -0.479
The regression equation is
Song sharing index = 46.6 - 11.0 Distance (t=5.55, p<0.001)

Figure 3.9. Song sharing indices as a function of distances in the Loch Garten population.



Song sharing index in percentage (arc-sin transformed). Distances in kilometer.

Correlation of Song sharing index and Distance = -0.639
The regression equation is
Song sharing index = 55.9 - 11.9 Distance (t=6.64, p<0.01)

Figure 3.10. Dendrogram showing the groupings of birds in the Tentsmuir population, based on the song sharing indices between them.
(Cophenetic correlation = r = 0.812;
t=14.124, df=103, p<0.01)

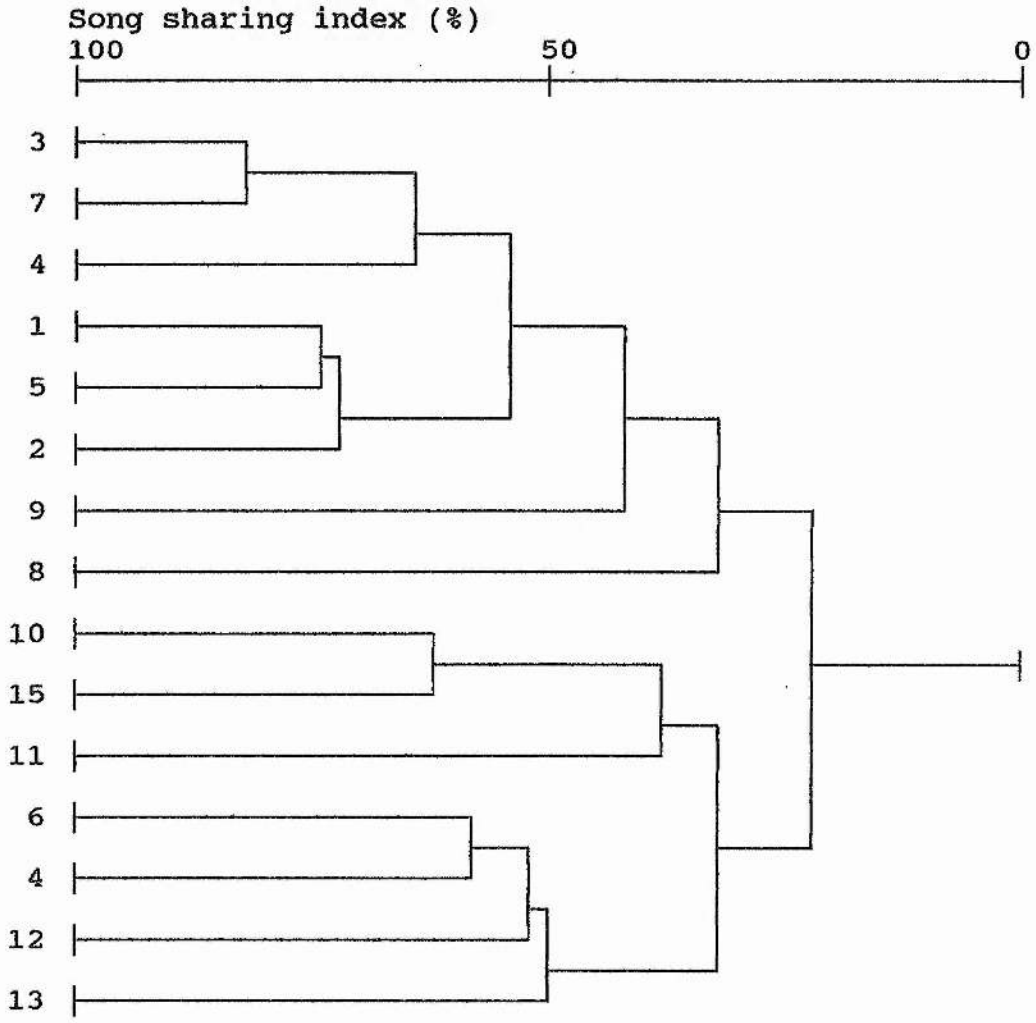


Figure 3.11. Dendrogram showing the groupings of birds in the Loch Garten population, based on the song sharing indices between them.
Cophenetic correlation (r) = 0.823;
(t=11.60, d.f.=64, p<0.01)

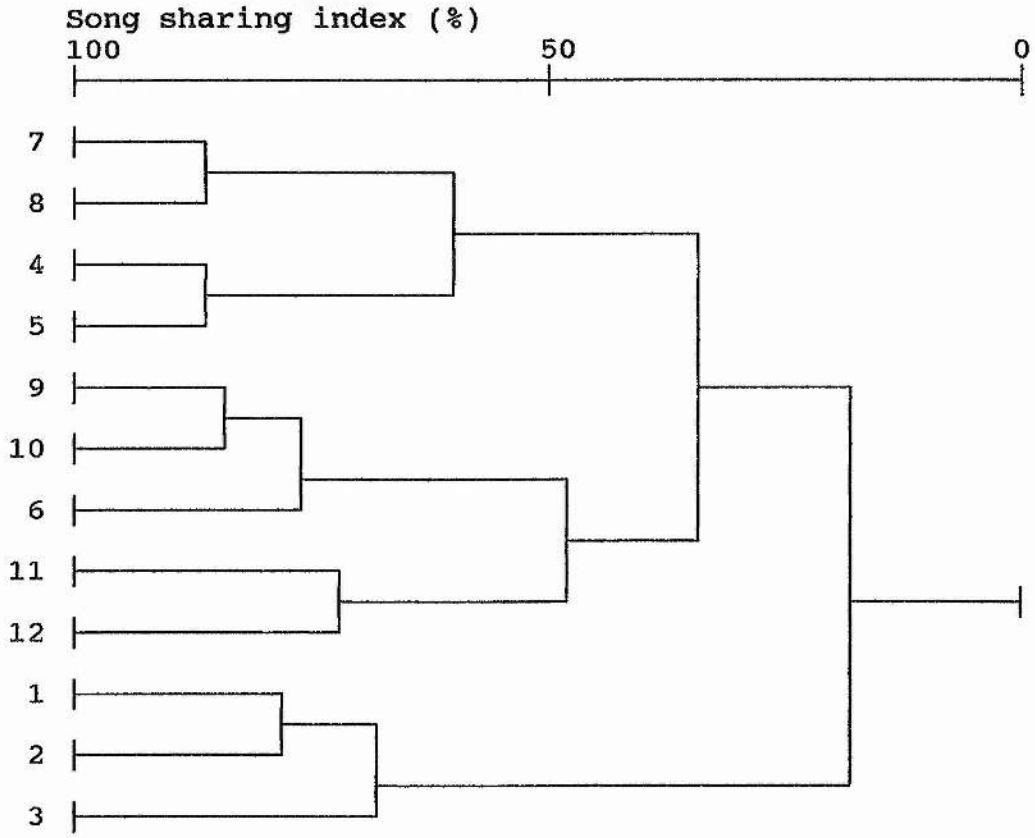


Figure 3.12. Position of birds in Tentsmuir and their grouping based on clusters in Figure 3.10.

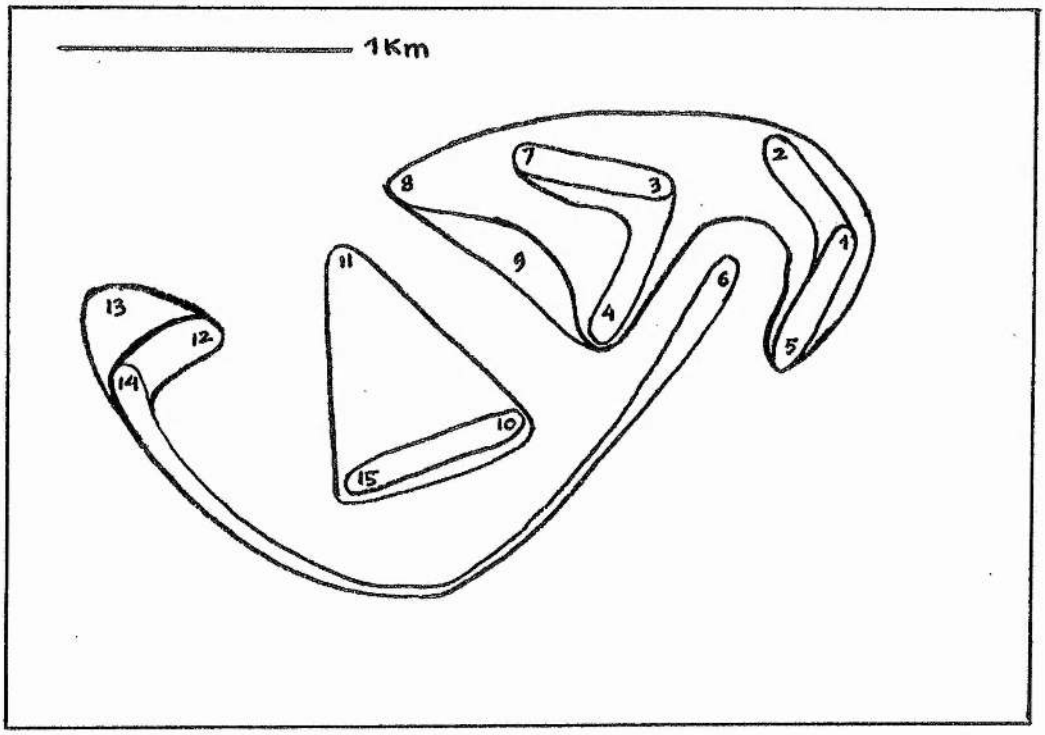
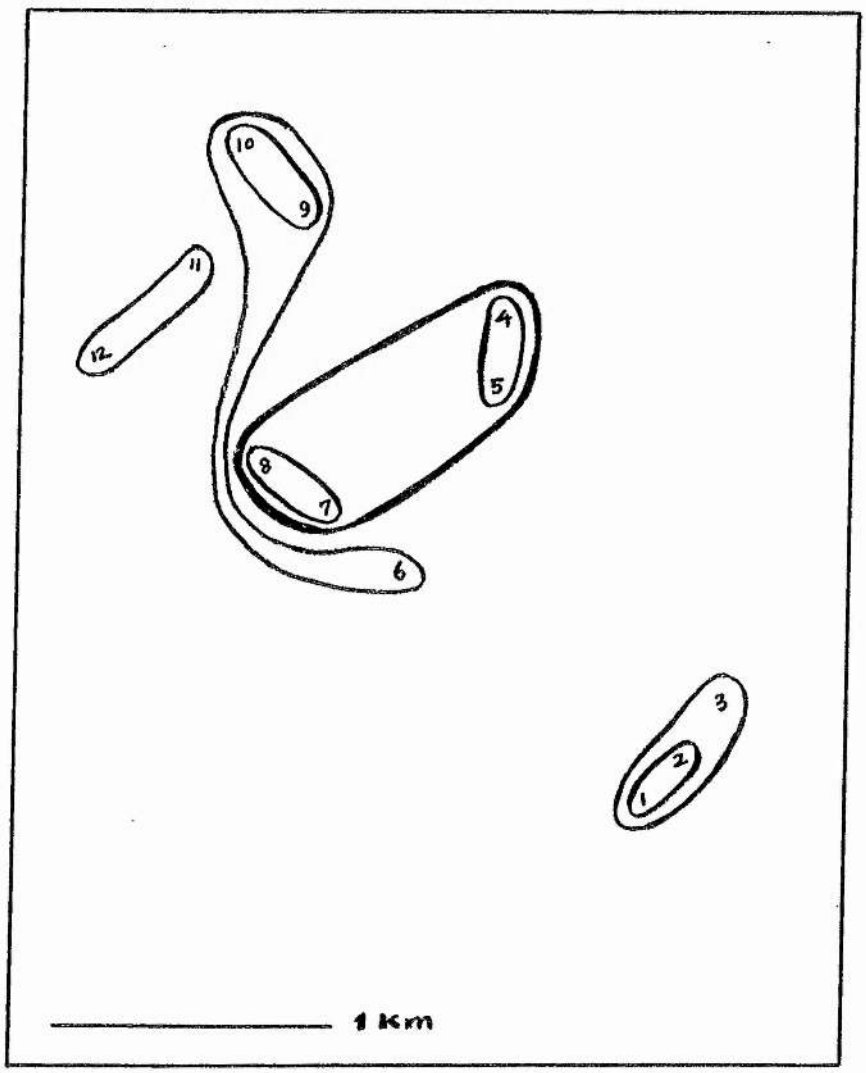


Figure 3.13. Position of birds at Loch Garten and their groupings based on clusters in Figure 3.11.



cluster analysis was carried out on the song sharing indices. Figure 3.10 and 3.11 show the dendrograms of individual groupings of birds in Tentsmuir and at Loch Garten, respectively.

From the dendrograms the groupings of birds were then plotted according to the position of birds within the study sites, and the results are shown in Figure 3.12 and 3.13. From these figures it appeared that based on the degree of their song sharing neighbouring birds in both populations were indeed grouped into the same clusters. There was, however, an exception for a particular bird from each population. At Tentsmuir there was one bird which was not clustered with its immediate neighbours (Bird 6 - Figure 3.12), and so was there at Loch Garten where one bird was clustered with birds further apart (Bird 6 - Figure 3.13). This may suggest that these particular birds were newly arrived to the area because they did not share more songs with their immediate neighbours. This suggests that song learning may take place both between neighbouring birds, so that they have more song in common than with birds further apart, and in their natal place before their dispersal to new sites where they breed.

DISCUSSION

The coal tit in both the Tentsmuir and Loch Garten populations showed similar repertoire sizes, although that of the Loch Garten population was smaller and was probably underestimated. The repertoire size in both populations varied considerably in that it ranged from 6 to 19 song types.

Despite this, there was no indication that any bird had a larger repertoire than expected by chance. It has been reported for great tits that repertoire size is related to fitness, such that males with larger repertoires are more likely to survive to breed and to have young than those with smaller ones (McGregor *et al.* 1981, Lambrechts & Dhondt 1986). A similar correlation has also been reported in other species such as mockingbirds, *Mimus polyglottos* (Howard 1974), *Acrocephalus* warblers (Catchpole 1980), and the red-winged blackbird, *Agelaius phoeniceus* (Yasukawa *et al.* 1980). The repertoire size in both populations of coal tits studied here varied a lot among individuals, and to what extent this affects their reproductive behaviour remains to be explored.

In most passerine species the number of songs a bird has in its repertoire is directly connected with song learning which is the mechanism of song-acquisition. It has been suggested that song learning can take place early in a bird's life or both before and after its dispersal (Kroodsma 1978, Slater & Ince 1982, McGregor & Krebs 1989). Song copying is a common phenomenon in song development. Slater *et al.* (1980) suggested that random events involved in song copying by young males as they disperse resulted in the random distribution of songs in chaffinch populations. The result showed that the number of birds singing any particular song type was randomly distributed. This might suggest that songs within the coal tit populations were randomly copied too, otherwise some song types would have been preferred by a number of birds and so represented disproportionately in the populations. There is also the possibility that a combination of particular song types might be preferred for copying. The results did not

support this idea since no particular combination of song types occurred in more repertoires than expected by chance. This has also been reported in other species, such as chaffinches (Slater *et al.* 1980) and great tits (McGregor & Krebs 1982).

Using ten characters of each song type as the basis of comparison between song types, there was a tendency for some of the song types from Loch Garten to be separated from those from Tentsmuir. To some extent, this might suggest geographic variation in coal tit songs. The results indicated that the possibility of similar song types occurring in the same repertoires was as much as that of occurring in different repertoires. This confirms the results found in Chapter 2 about the variability within repertoires. If similar song types were in the same repertoire, this would mean that the repertoire had less variability. Repertoires with less variability would not be effective in countering the habituation of other birds (Krebs 1976).

Song copying between neighbouring birds is a common phenomenon. This would allow males to share songs with their neighbours where they establish territories (Nottebohm 1969) and perhaps to occupy empty territories without engaging in conflicts with neighbours (Payne 1981, Slater 1981). The significance of being able to share songs with neighbours has been discussed earlier (see Introduction). It has been suggested previously that neighbouring birds are more likely to share more songs than those separated by some distance (e.g. McGregor & Krebs 1982, Morton 1987). The result obtained here did indeed show a strong negative correlation between the amount of song sharing and the distances between individuals :

the greater the distance between them the fewer songs they shared in their repertoires.

There was one particular bird from each population which shared more songs in its repertoire with birds further apart than with immediate neighbours. It is likely that this was the result of learning songs before their arrival in the area. This might support the idea that song learning can take place before dispersal.

If they were indeed newly arrived birds, the question now is to what extent these birds would copy the songs of their immediate neighbours. If they remain in the area in the following breeding season, this would be shown by the change in composition of their repertoires with time. As mentioned in Chapter 2, the study could not reveal such changes, if any, due to the lack of uniformity in recording efforts from year to year. It is possible that newly arrived birds copy neighbour's songs as they set up territories. But whether such a change occurs in coal tits, and whether it is influenced by a change in neighbourhood, remains to be explored.

Such a change would be related to song learning in adulthood. So far there is no information on whether coal tits can learn songs in adulthood. In great tits, McGregor & Krebs (1989) found that this species was able to learn songs throughout its life, and the repertoire composition changed with time but not the size of repertoire. They suggested that the change in repertoire composition was the result of changes in neighbourhood. In chaffinches, Goodfellow & Slater (1990) reported changes in songs from year to year although they questioned if chaffinches could learn in adulthood.

CONCLUSION

The size of coal tit repertoires varied considerably ranging from 6 to 19 song types, at least in the two populations studied here, but there was no indication that any individual had a larger repertoire than expected by chance. There was an indication that songs within the populations were copied at random, but no particular combination of song types was preferred for copying. It appeared that the possibility of songs with similar structures occurring in the same repertoires would be as much as of them occurring in different repertoires.

The results in this study suggest that song copying in coal tits might occur between neighbours as shown by the effect of distance on song sharing between birds : the greater the distance between them the fewer songs they shared in their repertoires. Song learning in coal tits might take place before dispersal as indicated by two birds that did not share songs with their immediate neighbours as much as with birds further apart.

Further information is necessary to reveal any association between the repertoire size in a coal tit and its reproductive success, to find out whether coal tits could learn when in adulthood, whether learning at this period would lead to a change in the repertoire composition with time, and whether such a change is associated with a change in breeding location.

CHAPTER 4.

SINGING PERFORMANCE

INTRODUCTION

Most passerine species sing more than one type of song. Several hypotheses have been put forward to explain the reasons why they have repertoires. The main proposals of these hypotheses are that repertoires: (1) enhance individual recognition, (2) are the result of sexual selection, (3) increase success in territorial competition, (4) include songs which serve different functions, and (5) are a way of avoiding exhaustion during territorial advertisement and female attraction.

It has been demonstrated that birds are able to discriminate individuals based on song features (reviewed in Falls 1982). Individual recognition has been investigated by testing for neighbour-stranger discrimination using playback since neighbour recognition may depend on individual recognition. In playback sessions territorial males usually react more strongly to stranger's songs than to the songs of immediate neighbours (Lemon & Harris 1974, Brooks & Falls 1975, Zach & Falls 1979). Brooks & Falls (1975) found that white-throated sparrows (*Zonotrichia albicollis*) used frequency as a cue in individual recognition. Previously Lemon & Harris (1974) suggested that in this species the frequency pattern within an individual was less variable than that between individuals, and this could indicate individual identity. Nelson (1989) also found that song frequency is used as a cue for individual recognition in field sparrows (*Spizella pusilla*).

In many species song is the most important means of sexual attraction (Catchpole 1979, 1987). In sedge warblers (*Acrocephalus schoenobaenus*) the male reaches a peak in singing activity before pairing, suggesting that song is

primarily a means of female attraction, and males with larger repertoires pair earlier than the males with smaller ones (Catchpole 1973, 1980). In mockingbirds (*Mimus polyglottos*) it has also been found that males with larger repertoires could acquire better quality territories and more advantage in attracting females over those with smaller repertoires (Howard 1974).

Other species in which a correlation between repertoire size and mating success or success in territory acquisition have been shown are, for example, great tits (*Parus major*) (Krebs 1977), canaries (*Serinus canarius*) (Kroodsma 1976), and redwinged blackbirds (*Agelaius phoeniceus*) Yasukawa *et al.* 1980). In canaries, tapes playing larger repertoires more strongly stimulated females to build nests and lay eggs than those with smaller repertoires (Kroodsma 1976). In redwinged blackbirds, males with larger repertoires pair earlier (Yasukawa *et al.* 1980); male great tits with large repertoires are more successful in acquiring larger territories (Krebs 1977).

In many species, to possess a territory is undoubtedly important for breeding. In species where males must hold territory before and after pairing, the ability to maintain territory is crucial. In most passerines song is generally acknowledged to function in territorial maintenance. Matched counter-singing with the opponent is a mechanism which is mainly used to keep away the opponent (Krebs 1977). In order for the birds to be able to match each other's songs they must have quite large repertoires. In keeping the opponent out of the territory, males with larger repertoires are more successful than those with smaller ones. The evidence for

this has come from great tits (Krebs *et al.* 1978) and redwinged blackbirds (Yasukawa 1981).

The effectiveness of repertoires in territorial maintenance is, however, related to the habituation of the listener. A particular song, or phrase, which is sung repeatedly over a period of time, is likely to lose its effectiveness as a signal due to habituation of the receivers (Hartshorne 1956). Great tits have been found to habituate more quickly to playbacks of simple songs than to repertoires (Krebs 1976).

Krebs (1977) further suggested the Beau Geste hypothesis, a mechanism by which repertoires could play a role in territorial maintenance. A male holding a particular territory should attempt to keep out floaters which are trying to obtain territories. A way of deterring such individuals might be to give them the impression that the territory is occupied by many males. This can be achieved by singing different songs if the bird has a repertoire. Krebs proposed that the mechanism for this assessment involved intruder habituation. An intruder would quickly habituate where fewer songs were heard in an area, and would eventually settle in the area.

In some species, different songs are also thought to signal different meanings. Lein (1978) found that chestnut-sided warblers (*Dendroica pennsylvanica*) used different types of songs in accordance with the likelihood that they would attack an intruder. Earlier, Morse (1970) found two song types in black-throated green warblers (*Dendroica virens*) which were used in different situations. In bridled titmice (*Parus wollweberi*) Gaddis (1983) found different song types to

occur in different contexts. However, in a number of species this is not the case (e.g. great tits, Krebs *et al.* 1978; redwinged blackbirds, Smith & Reid 1979).

Lambrechts & Dhondt (1988) proposed a new idea to explain the existence of song repertoires: the anti-exhaustion hypothesis. They suggested that, within a period of active singing, birds may be unable to maintain high song output because of exhaustion in the neuro-muscular system involved in sound production. However, they may overcome such exhaustion effects by switching songs regularly to other song types. As the new song type would require a different pattern of neuro-muscular coordination, changing to it would give the birds a chance to recover as well as allowing them to maintain high song output. Birds with large repertoires are more likely to succeed in maintaining high song output by switching song types as compared to those with smaller repertoires.

The study described in this chapter aims to test this last hypothesis on coal tits. This species has stereotyped song structures and individuals possess a repertoire of up to 16 song types (Latimer 1977, Göller 1987). Like the great tits studied by Lambrechts & Dhondt, on which their hypothesis is based, it seems an ideal species on which to test the idea. Earlier, in Chapters 2 and 3 it was shown that the repertoires of coal tits in the study sites ranged from 6 to 19 song types. The singing activity of this species also provides the possibility to test the hypothesis because a male sings a sequence of bouts of different song types during a period of singing.

METHODS

Male coal tits were recorded in 1989 and 1990 in Tentsmuir forest, Fife. Details about the study site are described in previous chapters. The analysis for this study, however, did not include the recordings from 1989. This is because the 1989 recordings did not cover all males in the area and the repertoire size of each male could not be ascertained. Spontaneous songs of 15 males were recorded between 06.30-10.30 hrs from late February to early June 1990. Although the birds were not colour-ringed, the identity of individual males was recognized because specific song posts were regularly used by each male, and also different males usually had quite distinctive songs. In order to minimize the possible effects of time of day on song output, the analysis in this study only included recordings made between 06:30-08:00 hrs.

A total of 68 song bouts were available for analysis. A bout is defined as a series of one particular song type which was recorded either from the start of singing activity or from the start of the new song type after switching from another type to the end of the series. The end of a bout could be due either to the cessation of singing activity, which was found to be the usual case, or to a switch to another type of song.

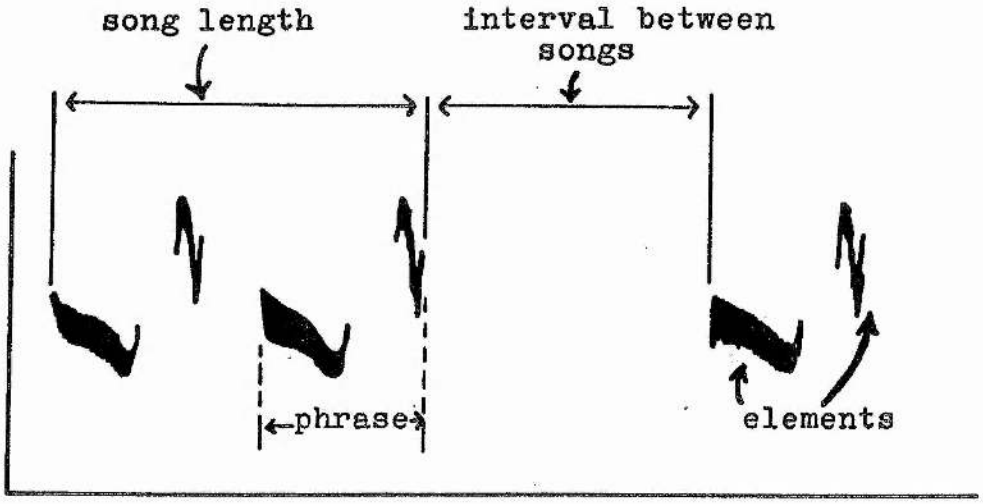
Detailed measurements from each bout were the same as those made by Lambrechts & Dhondt (1988). The numbers of **song-units** (see Figure 4.1) within each bout were counted. From each song the following variables were measured: (1) the length of the song, (2) the length of interval between songs, (3) the song-unit duration (i.e. the song length plus the length of interval between songs, (4) the percentage

performance time in each song-unit (i.e. the percentage ratio of the song length to the song-unit duration), and (5) the number of elements in each song-unit.

The measurements were taken directly from the screen of a DSP Sona-Graph model 5500 using the original recording speed with the aid of an Amstrad PPC640D-IBM compatible computer. A simple BASIC program, which made use of the timer facility in the computer, was used to measure the duration of the songs and inter-song intervals. On the sonagraph screen a cursor line was placed to mark the start of measurement. As a sonagram of a song-unit moved across the screen, and at the time when the beginning of that song-unit touched the cursor a key "S" on the computer keyboard was pressed to start the timing, and when the end of the song-unit touched the cursor a key "E" on the computer keyboard was pressed to end the timing. The computer then calculated the length between the pressing of keys S and E as the length of that song-unit. The same method was used in measuring the interval between songs. The number of song-units, which was taken as a measure of bout length, and the numbers of elements per song unit were counted directly from sonagrams on the DSP screen.

Lambrechts & Dhondt (1987, 1988) described a phenomenon called 'drift' in which the interval between successive song-units or phrases was found to increase towards the end of songs or bouts. It was on the basis of this phenomenon that they put forward their anti-exhaustion hypothesis. They pointed out that the longer the pauses, or intervals, between song-units, as well as the shorter the songs themselves, towards the end of a bout, the less the song output (measured as ***percentage performance time***) produced by a bird. They

Figure 4.1. A song of coal tit with variables measured in the study.



measured drift for each bout using the linear regression of percentage performance time with song number (or song-rank), the position of the song within the bout. A negative slope indicates the occurrence of drift. The analyses used to look for drift in the present study followed those of Lambrechts & Dhondt (1988).

The bouts analysed involved 23 song types and 15 males. Comparison of all measures between song types and between males was made using the mean values of all variables in each bout. Parametric correlation and regression analyses were carried out to investigate drift; but prior to the analyses on the percentage performance time data, the data were arc-sin transformed to obtain normal distributions. Kruskal-Wallis analysis of variance was used whenever possible. All statistical analyses were done using MINITAB Release 7.

RESULTS

All variables in all bouts were very variable. The bout length (=the number of song-units in the bouts) was the most variable with a coefficient of variation of 49.44%, and the percentage performance time the least variable (coefficient of variation = 14.35%). Using the mean values per bout, there were no significant differences between males in any of the variables measured (Table 4.1). This might suggest that all males have similar singing capabilities. The lack of difference between males in the percentage performance time suggests that there was no individual male effect on the percentage performance time in the bouts. The bout length was

similar between males, suggesting that all males produced a mixture of long and short bouts during the morning singing activity. In contrast to the similarities between males, there were strong differences between song types in all parameters measured (Table 4.2).

In only six of the 68 bouts recorded was there drift in the percentage performance time, i.e. a significant negative slope in the linear regression of the percentage performance time with song rank. Only one of these bouts showed a significant shortening of song duration with song rank. In the other five bouts there was a tendency towards shorter song duration combined with a significant shortening of the interval between songs.

Apart from the 6 bouts in which percentage performance time decreased, there were 10 which showed a significant increase in percentage performance time. Of these 10 bouts, 8 showed significant decrease in the interval between songs. This may suggest that the increase in percentage performance time is mainly due to the shortening of interval between songs. Of the 68 bouts, there were thus 52 without any significant change up or down in the percentage performance time. From these differences between bouts, the occurrence of drift in coal tits does not seem to be more than a chance occurrence.

Lambrechts & Dhondt (1988) found differences in the percentage performance time between bouts with drift and those without drift from the same males, with that of bouts with drift significantly higher than that of bouts without drift. Further, they found significant differences between the first 10 song-units of bouts with and without drift. The first 10

Table 4.1. Differences between males analysed with Kruskal-Wallis anova. (ns=not significant)

Parameter	range	H	df	
Bout length	7.00 - 54.00	10.61	14	ns
Song length	0.90 - 2.43	20.04	14	ns
Inter-song interval	0.84 - 4.75	21.13	14	ns
Song-unit duration	1.84 - 6.51	20.03	14	ns
Performance time	27.53 - 64.82	12.46	14	ns
Number of elements	4.30 - 16.12	12.12	14	ns

Table 4.2. Differences between song types analysed with Kruskal-Wallis anova. (* = $p<0.05$; ** = $p<0.01$)

Parameter	range	H	df	
Bout length	7.00 - 54.00	38.13	22	*
Song length	0.90 - 2.43	56.41	22	**
Inter-song interval	0.84 - 4.75	43.02	22	**
Song-unit duration	1.84 - 6.51	48.46	22	**
Performance time	27.53 - 64.82	36.19	22	*
Number of elements	4.30 - 16.12	58.81	22	**

song-units from bouts with drift showed higher percentage performance time than those from bouts without drift. They suggested that if a bird started to sing at higher output (i.e. percentage performance time) than average, it might end up with exhaustion, but if the bird started with lower output its performance might not show exhaustion. A similar comparison was made here on 5 males which showed bouts both with and without drift.

Table 4.3 shows the results of intra-male comparison of the mean performance time between bouts with and without drift. The percentage performance time of bouts with drift tended to be higher than that of bouts without drift, but no significant difference between them was shown. However, the sample size for this comparison was quite small.

One bout which showed drift consisted of only 8 song-units. In order to make a comparison between the performance at the beginning of bouts from the two categories, the first 5 song-units from each bout were sampled. The result of this comparison is shown in Table 4.3. It appeared that the percentage performance time of the first 5 song-units from bouts with drift was significantly higher than that from bouts without drift. The results might suggest that higher output at the start of the bout may lead to drift in the bout, even though the overall performance does not differ between the two categories of bouts.

In order to investigate whether switching song types is induced by the decrease of song output in the preceding bouts and can increase the song output in the following bouts, a comparison was made using 10 samples of song switching (i.e. 10 pairs of bouts between which song switching occurred).

Table 4.3. Comparison of the percentage performance time between bouts with and without drift from males which showed both categories of bouts. (ns=not significant; * = $p<0.05$)

	No.of Individuals	Percentage performance time (mean ± SE) With drift	Without drift	t
In whole bouts	5	53.09 ± 2.22	50.62 ± 3.14	0.57 ns
In first 5 song-units of the bout	5	60.95 ± 1.82	50.28 ± 2.98	2.73 *

Table 4.4. Comparison of the percentage performance time between the preceding bouts and the the following bouts from 10 samples of song-switching. (ns=not significant)

	No.of samples (bouts)	Percentage performance time (mean ± SE) Preceding	Following	t
In whole bouts	10	50.34 ± 2.22	49.50 ± 1.28	0.33 ns
Last/First 7 song-units of the bout	10	49.87 ± 2.85	50.88 ± 1.92	0.29 ns

First, the mean performance time of the preceding bouts was compared to that of the following bouts. Second, the mean performance time of the last 7 song-units in the preceding bouts was compared to that of the first 7 song-units of the following bouts. The mean song output in the preceding bouts was not expected to be different from that in the following bouts, because presumably the birds would maintain the same overall performance in both the preceding and following bouts. But the last 7 song-units in the preceding bouts were expected to be lower than the first 7 song-units in the following bouts, because the switching of song types was presumably caused by the decrease in song output in the preceding bouts, as predicted by the anti-exhaustion hypothesis.

Table 4.4 shows the results of this comparison and shows that there was no difference in the overall performance time in two consecutive bouts (i.e. the bouts of different song types which were produced one after another). There was a tendency that the last song units in the preceding bouts were lower in performance time compared to the first song units in the following bout, but the difference was not significant.

Earlier it was mentioned that the percentage performance time was the least variable among other variables measured in this study although the variability was quite high (CV = 14.35%). When the percentage performance time is plotted as a function of song rank within a bout, this variation is clearly shown. Such plots are here represented by pairs of bouts where song switching occurred (Figures 4.2 and 4.3). These figures show that the performance time varies a lot throughout the bout, and it also indicates that song switching is

not necessarily caused by exhaustion at the end of the previous bout.

DISCUSSION.

Of the 68 bouts analysed, only 6 showed a significant decerease in song output, i.e. showed drift in the percentage performance time over the whole bout. Of these particular bouts, only one showed a significant shortening of song duration through the bout, and none of them showed a lengthening in the interval between song-units through the bouts.

The remarkable differences between bouts and the fluctuation in performance time during bouts suggest that the occurrence of drift in coal tits is merely by chance, and when it occurs it is not caused by the prolongation of interval between songs in the bouts. This result contrasts with the findings of Lambrechts & Dhondt (1988) in great tits where 31 of 52 bouts showed drift, which was caused by the prolongation in the interval between songs in the bouts.

The anti-exhaustion hypothesis predicts regular switching of song types when a bird sings for an extended period of time. The switching of song types is regarded as a strategy to maintain a high song output. The results in this study showed that the percentage performance time of two consecutive bouts (where a bout of one song type switched to a bout of another) was similar to each other. This, however, would have been expected because the bird would be expected to maintain the same overall song output when singing a series of bouts.

Figure 4.2. Variation in song output of two consecutive bouts.

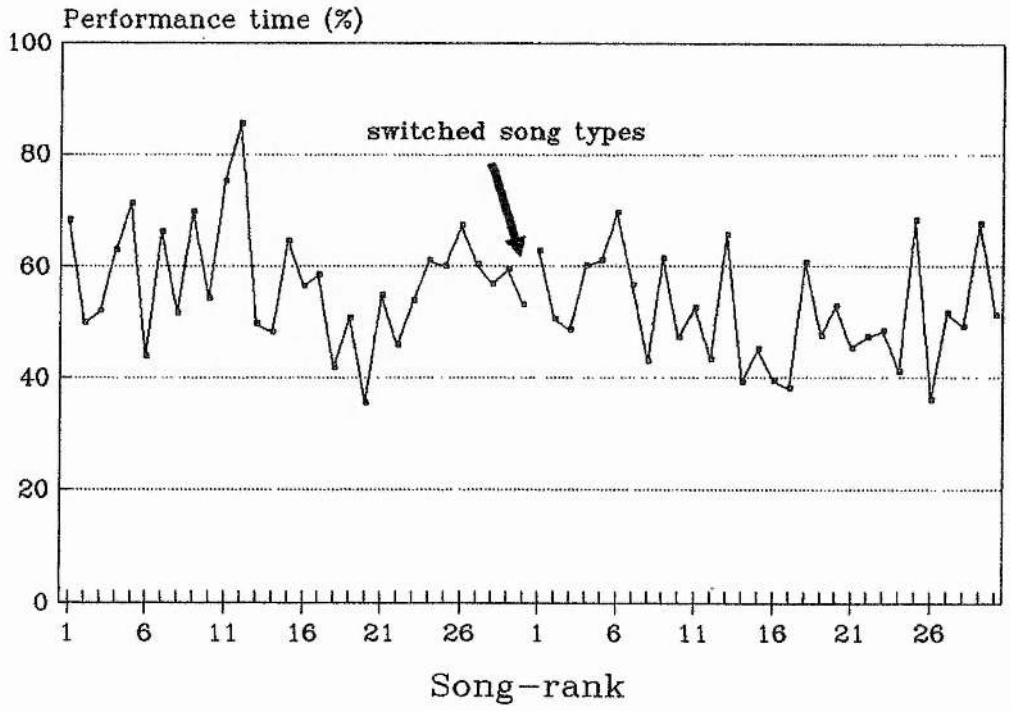
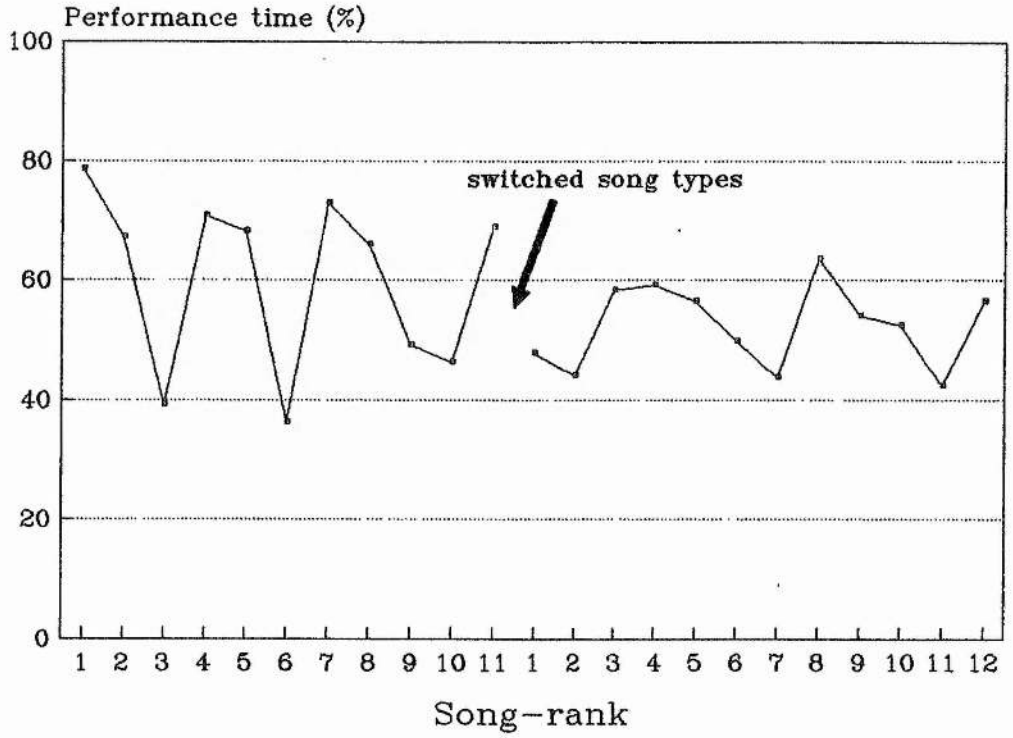


Figure 4.3. Variation of song output in two consecutive bouts.



Switching song type might occur because the song output in the last song-units of the preceding bout has begun to decline, and it might enable song output to increase again (i.e. for the first song units in the following bout to have higher song output). This, however, was not found in coal tits. There is no evidence that song switching in coal tits is related to exhaustion in the neuro-muscular systems involved in sound production.

Another approach to test the anti-exhaustion hypothesis is by playback experiments. Unfortunately, playback sessions done on coal tits failed to produce the long consistent responses necessary for testing the hypothesis. Weary *et al.* (1988) conducted playback experiments to test between the predictions that great tits would be unable to maintain a high song output when it has declined and to recover from such a decline they must switch song types, and that birds would be able to recover a high song output when they are motivated to sing.

Their first prediction was referred to the anti-exhaustion hypothesis proposed by Lambrechts & Dhondt (1988), and they predicted that any decline in song output shown by the birds between successive playbacks would not recover unless they switched song types. In the latter, they predicted that in a situation when external stimuli, such as playback songs, are increased, high song output could be recovered without a switch of song types.

They found that great tits were able to repeatedly increase their song output in response to playback stimulations, suggesting that the birds were unlikely to be exhausted, and that song switching was not followed by any

increase in song output. They, then, argued that playback had motivated the birds so that any increase in output due to switching might not be detected.

Lambrechts (1988) argued that exhaustion would occur only under particular conditions, especially at dawn when birds produce their highest song output. Weary *et al.* (1991) again carried out playback experiments at both dawn and later in the morning. The results of their experiments confirmed those found previously (Weary *et al.* 1988), in that song switching had no effect on song output, but they also supported those found by Lambrechts & Dhondt (1988) in that when singing is initiated with a high song output the decline in song output through the bout of singing is more likely to occur. This discrepancy may indicate that the occurrence of drift in song bouts may be merely by chance.

McGregor (1991) suggested that drift in great tits may not be entirely attributed to the changes in the interval between songs, as in those examined by Lambrechts & Dhondt (1988). He also showed a case in great tits where the occurrence of drift within a song unit was entirely caused by the prolongation of interval between phrases. The variability of the temporal characteristics of songs (e.g. song-length, phrase length, interval between phrases or between songs) that occurs in many species would make them vary in drift (McGregor 1991). In coal tits, the variability of phrase length and that of the length of interval between phrases may be equally likely to influence drift.

By examining song structures in great tits, Lambrechts & Dhondt (1990) found that variation within a repertoire was positively correlated with the size of the repertoire : the

larger the repertoires, the more the variability within them. Although their results contrasted to the anti-exhaustion hypothesis which predicts similar variation within both small and large repertoires, they suggested that such an increase was non-random in that larger repertoires included a high proportion of sound. Further, they suggested that constraints in singing ability affect the composition and/or the size of great tit repertoires, beside learning ability and opportunities to learn. Earlier in Chapter 2 it was found that the variability within coal tit repertoires was not associated with the size of repertoires. This may confirm the above prediction of Lambrechts & Dhondt (1990), but this does not seem to correlate with exhaustion during singing at an extended period.

CONCLUSION

The differences between bouts and variation of song output during the bouts of singing in coal tits seem to suggest that the occurrence of drift in this species is rare and probably due to chance. Song switching is predicted to enable birds to recover from drift (Lambrechts & Dhondt 1988), but there was no effect on song output of song switching in coal tits.

The variability within repertoires may facilitate the maintenance of high song output, hence avoiding exhaustion. Coal tits show a high variability of song characters within their repertoires (see Chapter 2), and this may be why drift could not be detected in this species.

CHAPTER 5.

SINGING INTERACTIONS : AN EXPERIMENTAL APPROACH

INTRODUCTION.

This study stems from the previous one reported in Chapter 4, in which it has been examined whether exhaustion in neuro-muscular coordination involved in song production may affect song output during an extended period of singing. This hypothesis suggests that song output declines as a bout of singing advances, and that the singer may switch to another song type so that his song output can be maintained because a new song type requires a different pattern of neuro-muscular coordination (Lambrechts & Dhondt 1988). Tests carried out by some authors (e.g. Weary *et al.* 1988, 1991) have failed to strongly confirm this idea.

The question examined here was : do birds perceive a singer with a declining song output as a weak individual ? If they do, the singer should avoid performing a bout of songs with a declining output. And, in a territorial contest, if a bird encounters an opponent singing in that way, we might expect him to ignore the opponent because there is no threat from the opponent. On the other hand, if the opponent sings a bout of songs with an increasing output he should regard the opponent as a threat and respond accordingly. Thus, singing performance could be used to assess vigour or potential fitness in rival males, and the experiments described here were aimed at testing this idea.

Song output is related to song rate, when song rate is defined as the number of songs delivered per unit time, measured as the ratio of song length to song length plus interval between songs (Lambrechts & Dhondt 1988, and see Chapter 4). It has been reported that song rate in willow warblers (*Phylloscopus trochilus*) was used to assess potential

threat (Jakobsson 1987). Jakobsson found a stronger response to be given by birds towards playback of rapidly repeated songs than towards those at a lower rate, and suggested that the birds perceived the songs at a higher rate as a serious threat.

In this study, the first playback experiment was carried out to test whether a bout of songs with declining output, i.e. decreasing song rate, would be perceived as indicating rival males of low fitness. The prediction was that the birds would respond less strongly with aggressive behaviour towards the playbacks of songs with declining output than towards those with increasing output. On the other hand, when they were confronted by songs with increasing output, they would also increase their own output. But to continuously produce high song output they might be constrained by exhaustion, and to avoid this they should switch song types more often.

Lambrechts & Dhondt (1987) have suggested that song length, or the number of elements making up a song, in great tits (*Parus major*) gives information about male 'strength' and/or male 'quality'. McGregor (1988) tested this idea on the chiffchaff (*Phylloscopus collybita*) using playback experiments. He predicted that the stimulation of a territorial intrusion by playback would stimulate the birds to sing longer songs. His findings contrasted with the prediction in that the birds were found to sing shorter songs during playback. The birds perhaps perceived the songs as a serious threat, and may have responded by signalling their willingness to attack. This depends, of course, on whether the shorter songs delivered during agonistic encounters signal intention to attack. Jakobsson (1987) has suggested that

shorter songs delivered by willow warblers during playback might signal such an intention. Other forms of aggressive behaviour may also be delivered, such as threat displays and warning calls prior to an attack when it is about to commence (Popp *et al.* 1990).

These considerations led to another question : do birds perceive long songs delivered by intruders as a more serious threat than shorter ones ? If they do, they would respond with more aggressive behaviour towards intruders singing longer songs than towards those singing short ones. This was tested using the simulation of territorial intrusion by playbacks of long songs and short ones.

METHODS

Two types of playback experiments were conducted. The first was conducted at Tentsmuir in April 1991, using a Marantz cassette recorder linked by 20 m of cable to a Nagra DSM loudspeaker which was mounted at about 1 m above ground level on a tripod. The second experiment was done at Loch Garten in May 1991 using the same cassette recorder linked by 20 m of cable to a pair of mini amplified Realistic SS20 loudspeakers. The loudspeakers were hung on a branch of a tree at about 1 m above the ground.

All playbacks consisted of a single 6 minute test, and the responding birds were recorded throughout the playback sessions. Whenever possible they were also recorded for as long as 2 minutes after the playback stopped, but most of the birds stopped responding as soon as the tape ceased. These

recordings were then analysed, and the measurements taken in the analysis were : (1) latency to vocal responses, (2) song unit (strophe) length, (3) pause length between songs, (4) percentage performance time (see Chapter 4 for definition), (5) number of songs, and (6) number of calls given during playbacks. The number of song types sung by the birds during playbacks was also registered to provide information about song switching. The two experiments were as follows :

Experiment 1.

Three experimental tapes, each with a different song rate, were prepared for each of three different song types. Each test lasted 6 minutes and was divided into three 2 minute periods. One test consisted of songs delivered at a normal rate throughout the 6 minute period. This rate of delivery was around that at which the birds sing territorial songs without the influence of an intruder. The number of songs on these experimental tapes averaged 24 songs per 2 minute period. The pauses between songs were set so that the song output throughout the tape was the same. These tapes were labelled as NORMAL songs. A second test used tapes of songs with declining rates. The first 2 minute period was at a high rate (averaged 40 songs), the second period was the same as the normal rate, whereas the third period was at a slower rate (averaged 18 songs). The song output of these decreased during the playback, and hence these tapes were labelled as DRIFTED song. The third set of tapes were the same as the second but with the rates in the reverse order : the first period was at a slower rate, the second period was at normal

rate and the third period was at high rate. These tapes were labelled as ACCELERATED tapes.

The three song types used in the experiments were taken from recordings of coal tit songs provided by the British Library for Wildlife Sounds (BLOWS) which were made in England. These were all typical coal tit songs. Altogether there were nine experimental tapes, i.e. three different song types with three different song rates. Although the experiments were not intended to test differences in coal tit responses to different song types, the inclusion of different song types was necessary to avoid the possibility of birds responding more to one song type than to another as suggested by Kroodsma (1989).

Initially, sites were chosen as places known from previous observations to be territories, and at each site it was intended to play the three tests of the same song type on different days. However, sites with a bird present on one visit were often found unoccupied on the next. Eventually the tests were done at sites where birds were found singing, and each site was visited only once. Each experimental tape was tested on three birds.

Experiment 2.

Two experimental tapes with different song lengths, i.e. a different number of elements in a song, were prepared for each of three different song types. Each of the experimental tapes was again used for 6 minute tests. The first experimental tape consisted of a series of four-phrase (syllable) songs with the same pause length between songs to give a constant rate of song delivery. The second

experimental tape consisted of a series of eight-phrase songs also with the same pause length between songs. The pause length on the second tape was twice as long as that on the first so that the song output of the two tapes was the same. The first tape was labelled as SHORT song, and the second as LONG song.

The three song types used were also taken from the recordings provided by BLOWS as mentioned above, and the tapes was prepared with the DSP Sonagraph, so that the length of pause between songs could be measured and re-recorded for experimental songs. Altogether there were six tapes, and each was tested at four sites where a bird was found singing in each site. Each site was only visited once, and vocalizations of the responding birds were again recorded during the 6 minute playbacks.

All statistical analyses for the results of the playback experiments a two-way analysis of variance and a mixed model analysis of variance carried out with Minitab R.7.

RESULTS

Experiment 1.

The variables measured from the recordings were latency to the first vocal responses, song unit (strophe) length, interval between songs, song output (measured as the percentage performance time once the song had started), the number of songs given as response, the number of song types sung during playbacks, the number of calls given as responses. Series of songs delivered by the birds as responses during

playback, which were supposed to indicate bouts of singing, were always interrupted by calls. This made it difficult to quantify the changes in song output and to compare them between different tests. The switch from songs to calls might help the birds to recover exhaustion, if it occurred, so that the song output might not change at all. Comparison was, then, made on the average song output between tests.

A two-way analysis of variance was applied for each variable to test whether the score of each variable differed between experimental tapes and/or song types used in the playbacks. No significant effect of song types was found on all variables. From all the variables, only the number of songs, the number of song types sung, and the number of calls showed significant differences between the experimental tapes. On the scores of the number of songs and those of the number of calls, the anova was redone using a mixed model to include the 2-minute periods during the playbacks. This was to test whether the scores were different between experimental tapes and the three different periods during playbacks.

Neither the song unit length nor song output was affected by the experimental tapes, although it appeared that the song unit length during the playback of accelerated songs was marginally shorter than during playback of normal and drifted songs, and the average song output during playback of drifted or accelerated songs was higher than that during playback of normal songs (see Figure 5.1).

The number of songs sung during the playbacks was significantly different between the experimental tapes ($F_{2,54}$ =11.50 $p<0.01$) and between the 2-minute periods during the playbacks ($F_{2,54}$=11.98 $p<0.01$). But it was not significantly

different between the song types ($F_{2,54}$=1.03 p=0.36). No effect of interaction between the experimental tapes, song types and the 2-minute periods was found on the number of songs sung during the playbacks. Figure 5.2 shows the mean number of songs during the playbacks.

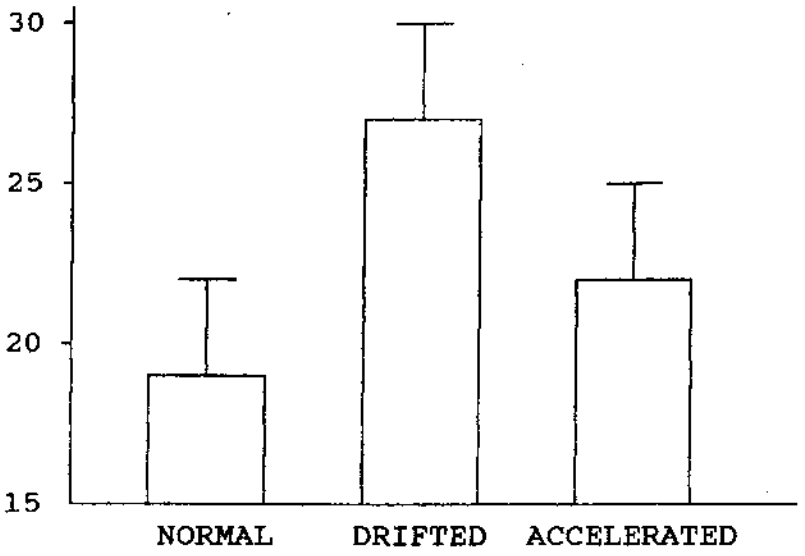
It appeared that songs were more frequently delivered during the playbacks of DRIFTED songs and less fequently during the playbacks of ACCELERATED songs. During the third 2-minute period of the playbacks, songs were less frequently delivered than during the other periods. The period during which the songs were the least frequently delivered was the third 2-minute period of the playbacks of ACCELERATED songs.

The number of song types sung during the playbacks indicated song switching. The number of song types was significantly different between the experimental songs ($F_{2,18}$ =6.64 p=0.01), and there was a tendency for the playback song type to affect the number of song types sung during the playbacks ($F_{2,18}$=3.36 p=0.06). Figure 5.3 shows the number of song types sung during the playbacks of the three experimental tapes. It appeared that the number of song types was less during the playbacks of ACCELERATED songs, and this indicates that song switching was more frequent during the playbacks of NORMAL and DRIFTED songs than during those of ACCELERATED songs.

The number of calls delivered during the playbacks was significantly different between the experimental tapes ($F_{2,54}$=22.00 p<0.01) and between the 2-minute periods during the playbacks ($F_{2,54}$=11.23 p<0.01). But it was not significantly different between the song types ($F_{2,54}$=0.82 p=0.456). There was an effect of interaction between

Figure 5.1. Mean song unit length and song output (percentage performance time) during playbacks of three experimental tapes at Tentsmuir. (Mean ± sd; N=9)

a) Song output (percentage performance time).



b) Song unit length (seconds).

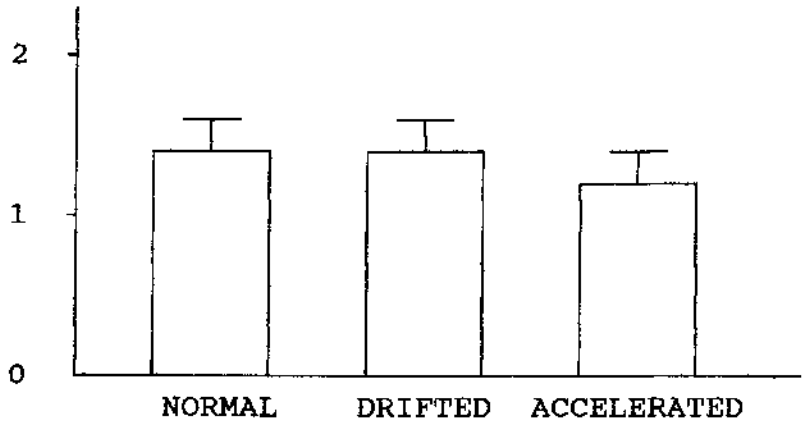
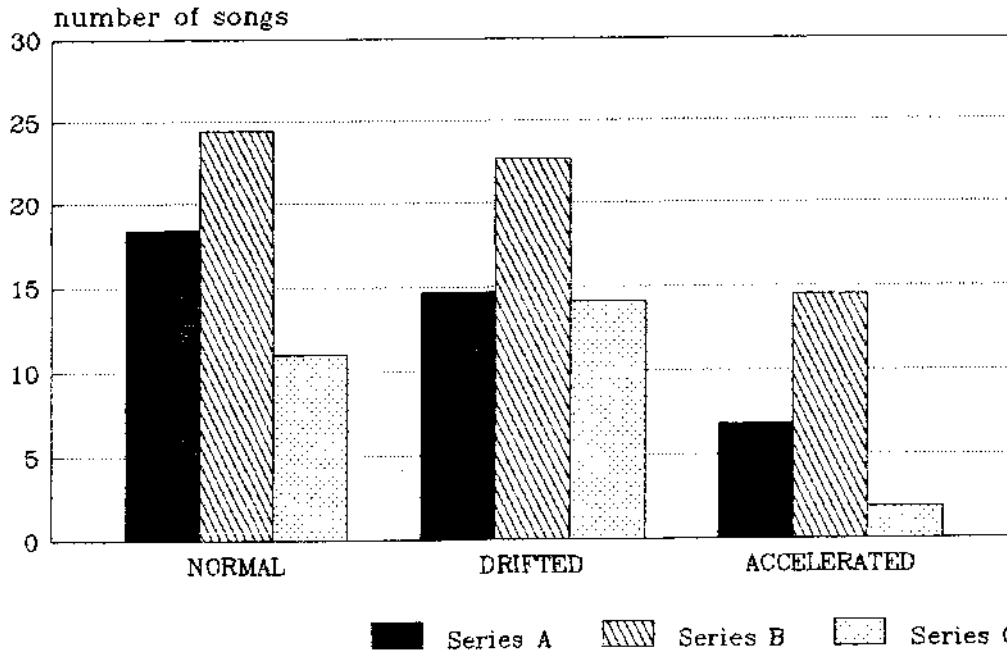


Figure 5.2. Mean number of songs during playbacks of three experimental tapes at Tentsmuir.



-Series A = First period.
-Series B = Second period.
-Series C = Third period.

Figure 5.3. Number of song types during playbacks of three experimental tapes at Tentsmuir.

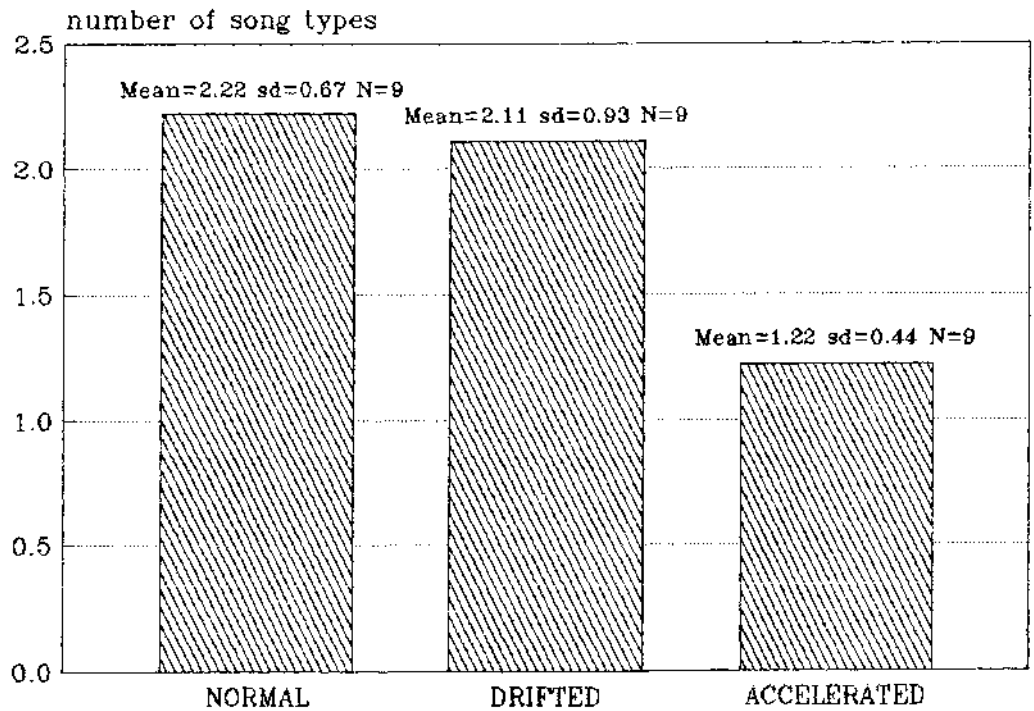
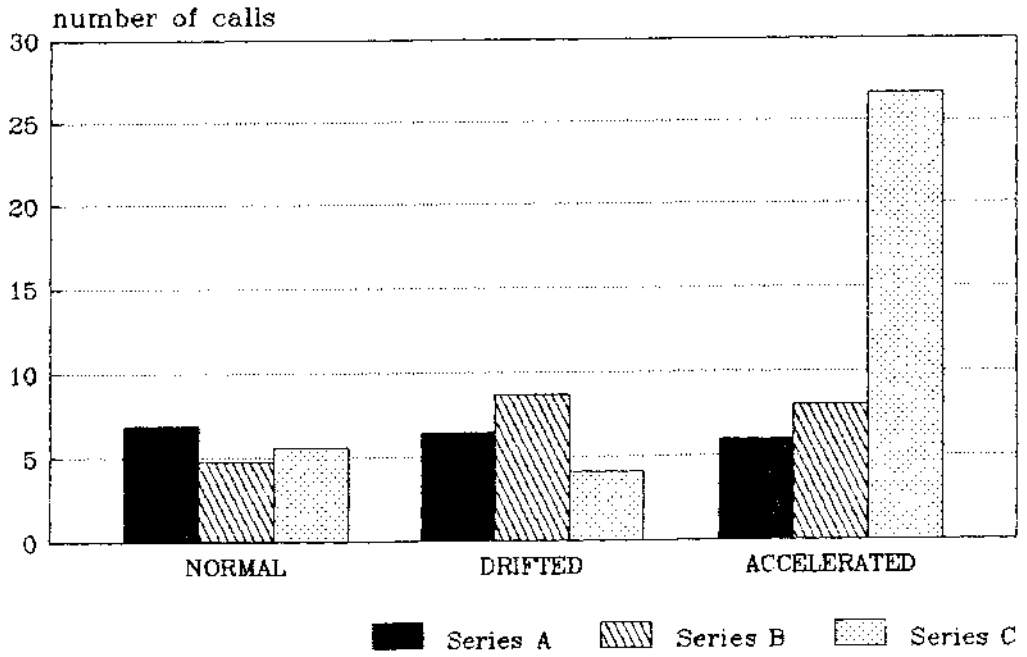


Figure 5.4. Mean number of calls during playbacks of three experimental tapes at Tentsmuir.



-Series A = First period.
-Series B = Second period.
-Series C = Third period.

experimental tapes and periods ($F_{4,54}$=21.12 $p<0.01$) on the number of calls. Figure 5.4 shows the mean number of songs during the playbacks.

It appeared that calls were, on average, more frequently delivered during the playbacks of ACCELERATED songs and less fequently during the playbacks of the others. The period during which the calls were substantially delivered as response was during the third 2-minute period of the playbacks of ACCELERATED songs.

Experiment 2.

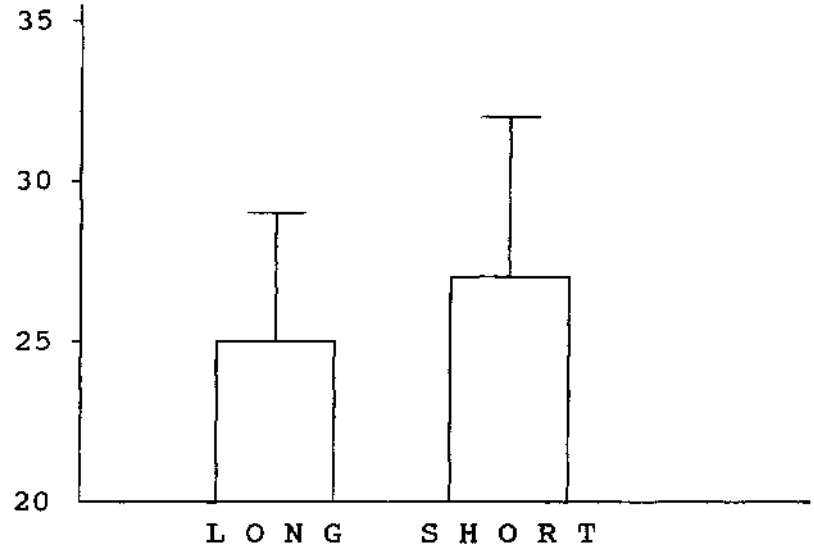
The variables measured from the recordings of responding birds were the same as in the first experiment. Comparison of song output between tests was, as in the first experiment, done on the average value. A two-way analysis of variance was also applied for each variable to test whether the scores for that variable differed between the two experimental tapes and/or song types used in the playbacks. Of all the variables, only the number of songs, the number of song types sung, and the number of calls showed significant differences between the experimental tapes but no significant effect of song types was found on any of the variables.

The experimental tapes did not significantly affect song unit length and song output, although the song unit length was slightly longer and the song output was lower during playback of long songs than those during playback of short songs (see Figure 5.5).

The number of songs produced during the playback was significantly different between the two experimental tapes ($F_{1,18}$=9.03 $p<0.01$), but the difference was not significant

Figure 5.5. Mean song unit length and song output (percentage performance time) during playbacks of two experimental tapes at Loch Garten. (Mean ± sd; N=9)

a) Song output (percentage performance time).



b) Song unit length (seconds).

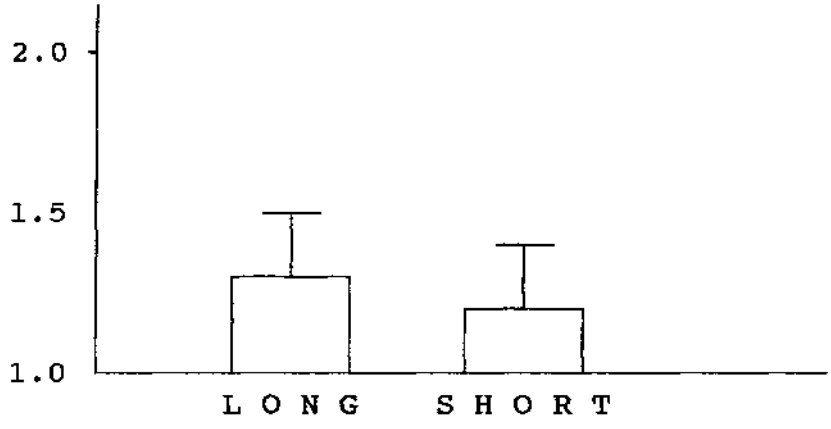


Figure 5.6. Number of songs during playbacks of two experimental tapes at Loch Garten.

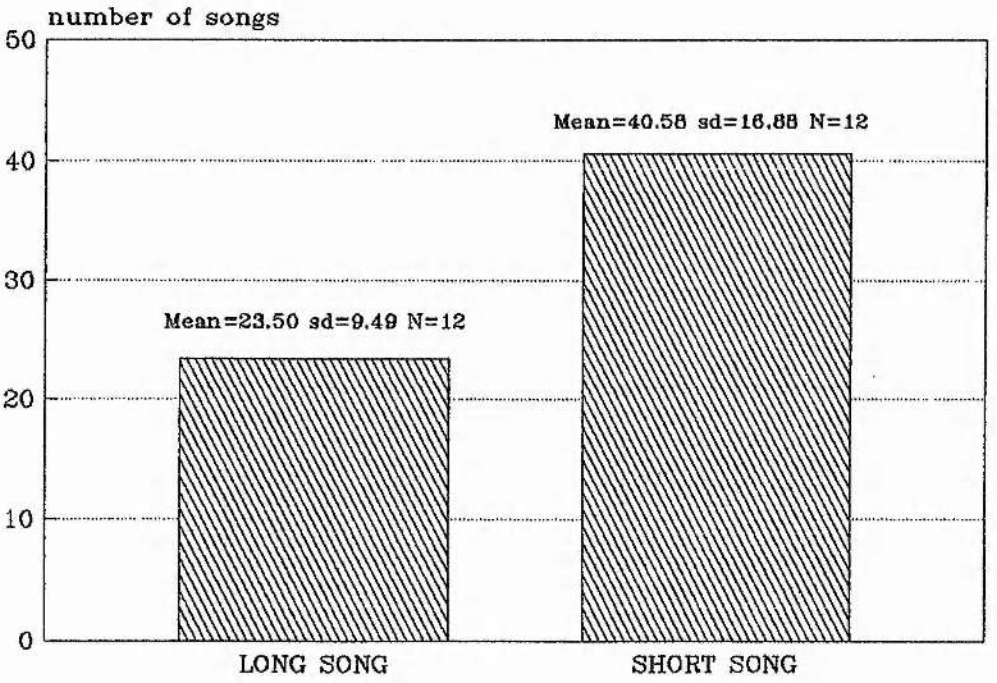


Figure 5.7. Number of song types during playbacks of two experimental tapes at Loch Garten.

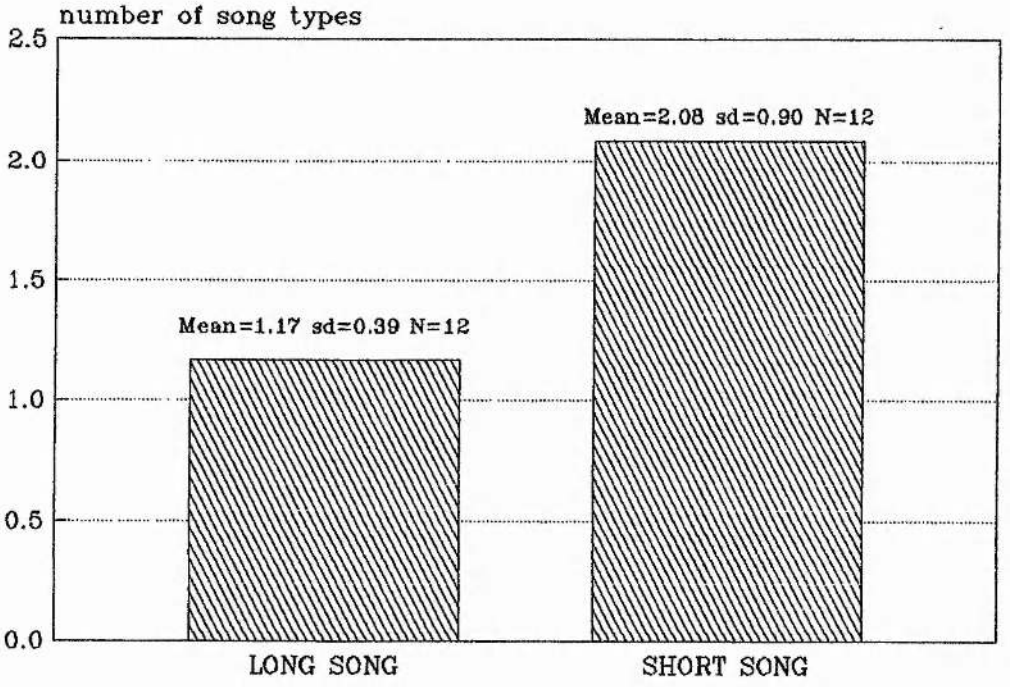
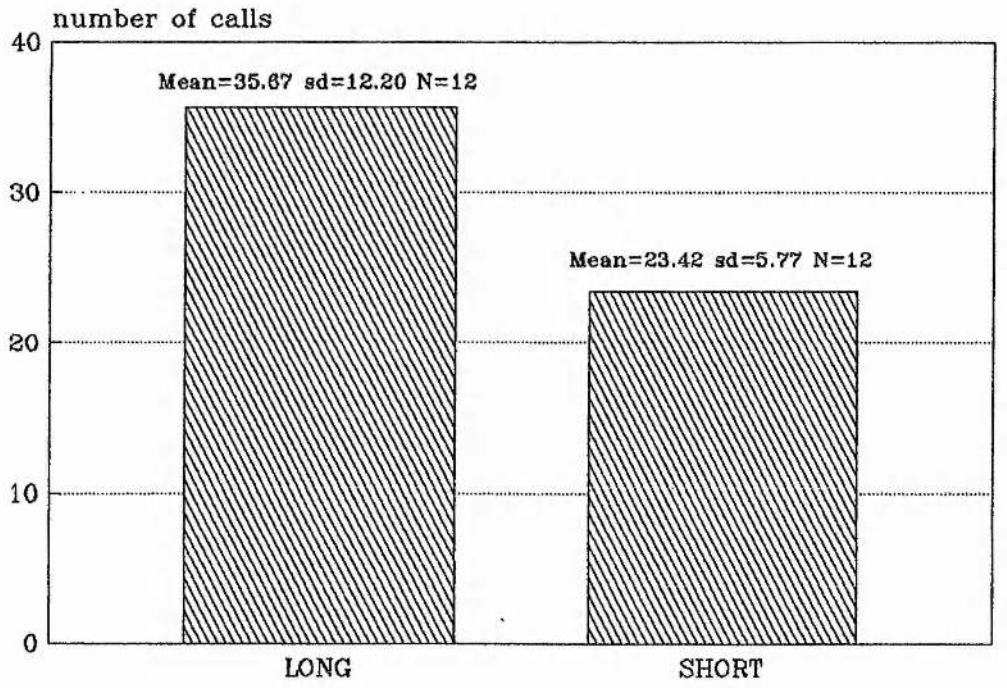


Figure 5.8. Number of calls during playbacks of two experimental tapes at Loch Garten.



between song types ($F_{2,18}$=0.10 p=0.90). Figure 5.6 shows the number of songs during the playbacks. It appeared that songs were more frequently delivered as response during the playbacks of SHORT-song tapes.

Differences in the number of song types sung during the playbacks between the two experimental tapes were also significant ($F_{1,18}$=10.37 p<0.01). Figure 5.7 shows the number of song types sung during the playbacks. In terms of the frequency of occurrence, song switching appeared to be more frequent during the playbacks of SHORT-song tapes than during those of LONG-song tapes.

The number of calls delivered as response during the playbacks was significantly different between the two experimental tapes ($F_{1,18}$=11.80 p<0.01), but it was not different between the song types ($F_{2,18}$=1.85 p=0.18). Figure 5.8 shows the number of calls delivered during the playbacks. It appeared that calls were more frequently delivered during the playbacks of LONG-song tapes.

DISCUSSION.

The results can be summarised as follows. In the first playback experiment, the song rates significantly affected the vocal responses given by the birds. The playbacks of songs with accelerated rate, showing an increase in song output, significantly inhibited the songs of responding birds, but induced more calls given as responses. During the third 2-minute period of the playbacks of accelerated songs, when the song rate was at peak, the number of calls delivered was

enormously increased. Song switching occurred more often during the playbacks of songs with normal or drifted rates than when the songs with accelerated rate were played. In the second experiment the number of songs produced during the playback of shorter songs was significantly greater than that when longer songs were played. But the number of calls was significantly greater during the playbacks of long songs. Song switching during the playbacks of short songs was significantly more frequent than during that of long songs.

It seems that coal tits respond to the simulation of a territorial intrusion using playback with both songs and calls. It is unfortunate that behaviour such as threat display could not be recorded, but calls were presumably delivered as warning against intruders.

During the playback of songs with increasing output, birds were observed trying to keep up with the rate of songs in the playback, but when the song rate in the playback became higher they seemed to give up and started giving calls. The result was that they spent more time giving warning calls during the period when song rate in the playback was at its peak, suggesting that they were signalling their aggressiveness. They may have perceived songs in the playback as being delivered by seriously threatening rival males, so that they responded with an aggressive signal. The prediction that birds would more strongly respond with aggressive behaviour towards playback of increasing output was thus supported. In black-capped chickadees (*Parus atricapillus*) calls are used as agonistic signals in a series of agonistic displays between two males, and the likelihood of agonistic escalation was determined by the performance of the two

contesting birds (Popp *et al.* 1990). It is likely that coal tits also perform such display related calls, and two confronting birds assess each other's strength from each other's performance. Aggressive displays would permit confronting individuals to assess each other, allowing them to avoid fierce confrontation such as fighting, when they are unlikely to win (Zahavi 1977).

During this playback experiment song switching was less frequent than during the playback of drifted or normal songs. It has been suggested that to avoid exhaustion birds should frequently switch song output (Lambrechts & Dhondt 1988). The results here run counter to this idea. This might be because the birds perceive the playback of increasing output as being an intruder posing a serious threat, so that signalling a warning might be better for them than matching song output and switching song types. In other species, agonistic encounters involve song switching. Kramer & Lemon (1983) and Kramer *et al.* (1985) suggested that song switching in song sparrows (*Melospiza melodia*) was related to stimulus intensity.

The prediction that the birds would respond with more aggressive behaviour towards the playback of long songs than towards short ones was supported. Lambrechts & Dhondt (1987) suggested that song length signals male 'strength' or male 'quality'. If intruders singing long songs were perceived as fitter males, so that they were a greater threat, the coal tits appeared to respond with a more aggressive signal, and thus the idea that song length is indicative of male 'strength' was supported.

During the playbacks of short songs the birds delivered more songs than during those of long songs. This may suggest

that the birds try to match the rate of songs in the playbacks. That the birds switched song types more often during the playback of short songs than during those of long songs might not necessarily be associated with exhaustion since the average percentage performance time was not significantly different between the two experimental tapes.

Calls were often delivered during the playback of the two experimental tapes, suggesting that the birds perceived the songs in the two playbacks as a threat. That the calls were delivered more frequently during the playback of long songs suggests that they are perceived as a more serious threat, so that signalling aggressive behaviour might be better than matching the song length of intruders. This situation may be analogous to the situation during the playback of songs with increasing output.

In natural agonistic encounters, individuals confronting each other may accumulate information about asymmetries in each other's strength before making decisions to escalate or to withdraw. This was revealed in black-capped chickadees (Popp *et al.* 1990), which performed agonistic displays during agonistic confrontation. Two confronting individuals assessed each other with calls, head-up display and a series of movements involving changes in the orientation between the individuals referred to as ballet. During ballet the individual which faced away from its opponent tended to lose, and withdraw from the confrontation. This may suggest that ballet provides information about the strength of opponents. Such displays may well be performed by coal tits during territorial confrontation, whereby they assess each other's fighting potential before deciding to continue or withdraw

from the confrontation. This, however, remains to be revealed.

CONCLUSION.

It was indicated that coal tits perceived the playbacks of songs of different rate and length as being intruders of different threats. The playback of songs with increasing rates appeared to be perceived as intruders of more serious threats than those of normal or drifted rates. The playback of long songs also appeared to be perceived as being intruders of more serious threat than those of shorter ones.

Further investigation on the behaviour of coal tits during agonistic encounters seems necessary in order to provide information about aggressive displays involved in such situations and the strategy they use in resolving agonistic situations.

CHAPTER 6.

GENERAL CONCLUSION

Some of the findings in this study have provided support for several hypotheses concerning the functional importance of song, especially in coal tits, but some others need further studies in order to obtain more evidence.

Several hypotheses have been put forward to explain the functional significance of song repertoires (reviewed in Krebs & Kroodsma 1982). One of those is the habituation hypothesis which proposes that repertoires are important in countering habituation in other birds, and predicts that songs within a repertoire would have a higher variability in their characteristics than those between repertoires (Krebs 1976).

Evidence for this hypothesis has come from great tits (*Parus major*) and varied thrushes (*Zoothera naevia*). Krebs (1976) found a greater variability of phrase length in the great tit songs within repertoires than that between repertoires. Whitney (1981) found in varied thrushes that the dominant frequency and period of modulation were more variable within repertoires than between repertoires. In this study (Chapter 2) several song characters were measured, namely the number of elements in a song, song length, phrase length, interval between phrases, the highest and lowest frequencies in a song, the average and range of frequency in a song, proportion of sound in a phrase and that in a song. All song characters measured showed a greater variability within repertoires than between them. This supports the hypothesis.

Further, it was found that song characters in the two coal tit populations studied were different, in that the birds in Tentsmuir sang with shorter temporal features and with higher pitch characters in their songs. Krebs & Kroodsma (1982) suggested that vocal variation between populations may

arise when they are isolated from each other. Birds in the two populations will certainly have developed their songs independently from each other, and thus such differences may be expected. Further studies, however, seem necessary in order to provide information about the various factors which may have led to such differences. The acoustic characteristics of the habitat are thought to play an important role in the evolution of avian vocalizations (Morton 1975). Martens (1990) found that birds living near Himalayan torrents avoided vocalizations with low frequencies, and suggested that habitat noise may act as selective pressure in the shaping of vocalizations of these birds. Habitat noise probably played an important role in the shaping of coal tit songs in the two study sites examined here. An investigation of differences in habitat noise in the two places is desirable since in this way the association between habitat noise and the song structures could be investigated in more detail. The common occurrence of another congeneric species (i.e. crested tits, *Parus cristatus*) at Loch Garten but not in Tentsmuir may induce character displacement in the songs of the two species. This remains to be investigated. The congeneric species present in Tentsmuir were great tits (*Parus major*) and occasionally blue tits (*Parus caeruleus*). The extent to which they associate with each other and whether such an association, if any, influences the shaping of their songs remains open for investigation.

Coal tits in the two study sites have a quite large repertoire, ranging from 6 to 19 song types (Chapter 3). There was an indication that songs within the population were copied at random, and that no particular combinations of song types

were preferred for copying. It was also found that the probability of songs with similar structures occurring in the same repertoire was the same as that they would occur in different repertoires. In great tits, males with larger repertoires are more likely to produce young surviving to breed than those with smaller ones (McGregor *et al.* 1981). The most likely reason for such an association between repertoire size and reproductive success, is that males with larger repertoires obtain better quality territories (McGregor *et al.* 1981). In coal tits, such an association remains to be explored, and detailed studies of a marked population seem necessary to provide further information. This was not possible during the course of this study because of the limited time available. Nest-boxes were present in both study sites and might have helped to make it possible to study the association mentioned above. However, coal tits made little use of the nest-boxes, and to locate their nest-sites took a considerable length of time. They are also hard to catch and mark as they stay in the canopy for most of their activity, even in response to playback.

Song acquisition in birds usually involves learning. It has been suggested that song learning can take place early in a bird's life or both before and after its dispersal (Kroodsma 1978, Slater & Ince 1982, McGregor & Krebs 1989). Neighbouring coal tits in the two study sites were found to share more songs than those farther apart (Chapter 3). This may indicate that song copying may occur between neighbours. Changes in neighbourhood may induce song copying between territorial birds and their newly-arrived neighbours. Some birds, however, shared little with their neighbours, and this

may indicate that song copying may not occur between them, or perhaps, that these birds were newly-arrived individuals whose songs were learnt before their dispersal so that they had not yet copied the songs of their neighbours. This needs further clarification, and detailed studies on marked individuals seem necessary.

Recently, a new idea was proposed in order to provide causal and functional explanation of song repertoires. During an extended period of singing, a bird may show a drift, i.e. a declining output of songs in a bout of singing due to exhaustion in the neuro-muscular coordination involved in song production. It was suggested that to recover from such a decline the bird must switch to another type of song which requires a different pattern of neuro-muscular coordination, but to do this he must of course have a repertoire (Lambrechts & Dhondt 1988). However, drift is rare in coal tits, and when it occurred it was probably due to chance (Chapter 4). There was no indication that song switching was caused by drift. Weary *et al.* (1988) tested this idea on great tits, the species on which the original hypothesis was based. They used playback experiments in order to test the prediction that switching song types was caused by drift, and they failed to find concrete evidence supporting the prediction. Lambrechts (1988) argued that drift would only occur under certain conditions, particularly at dawn when birds produce their highest song output. Weary *et al.* (1991) again tested the hypothesis using playback experiments carried out at both dawn and later in the morning. Their results showed a discrepancy in that they neither supported nor rejected the hypothesis. This has given rise to a crucial question : do birds really

perceive drift in a song bout as an indication of the 'strength' or 'quality' of the singer ? This question was tested on coal tits in this study (Chapter 5). There was no indication that drifted songs were perceived by the birds as being different from normal songs in the playback, but the playback of accelerated song rate, hence accelerated song output, appeared to be perceived as a more serious threat, and thus perhaps as indicating a fitter intruder (see below). It would be interesting to find out whether drift is related to male quality. Playbacks of song bouts with and without drift to females could be carried out, with the prediction that females would be less responsive to the playback of song bouts with drift than to those without drift. It this was the case, natural selection might favour those without drift, to the limit of the physical capabilities of the birds, so that drift in song bouts might never be detected.

Using playback experiments some interesting features of singing interaction in coal tits were revealed (Chapter 5). Coal tits appeared to perceive bouts of songs produced at different rates, or different song output, as being delivered by intruders posing different degrees of threat. There was an indication that the bouts of songs of increasing rate were regarded as intruders of more serious threat than those of normal or decreasing rates. There was also an indication that playbacks of long songs were perceived as a more serious threat than those of shorter ones. If the playback of accelerated songs was perceived as being delivered by fit intruders, the birds should respond more aggressively towards it. The results support this prediction, although there was no indication that responses given to the playback of drifted

songs were different from those of normal songs. Birds did not switch song types more often in response to the playback of accelerated songs than to that of normal or drifted songs, and this may be in contrast to the anti-exhaustion hypothesis which predicts that birds would switch song types when exhausted. This may substantiate the findings that drift is a rare phenomenon in coal tits.

The suggestion made by Lambrechts & Dhondt (1987) that song length is indicative of male 'strength' or male 'quality' appeared to be supported. This is in contrast to the results found in the chiffchaff by McGregor (1988). He predicted that the simulation of an intrusion using playback would stimulate the birds to sing longer songs. His prediction was not supported by his findings in that there was no indication that the birds showed longer songs in response to playback. If the songs in the playback were perceived as a serious threat, the birds might not match the length of songs in the playback, or perform longer songs than those in the playback as if signalling better 'quality' or 'fitter' opponents. He did not observe changes in the aggressive behaviour of chiffchaffs towards the playback.

Coal tits responded to playback with both songs and calls regardless of the rate of singing or the length of the songs in the playback. Calls delivered during playback were most likely to signal a warning towards intruders. It is likely that coal tits perform various displays during agonistic encounters, from which the likelihood of aggressive escalation could be detected. The black-capped chickadee uses calls as aggressive signals in a series of agonistic displays between two confronting individuals, and the performance of the two

males determines the likelihood of agonistic escalation (Popp *et al.* 1990). Further investigation on the behaviour of coal tits during agonistic situations would be interesting since it may provide information about the aggressive displays used during agonistic encounters and how such interactions are resolved. It might also reveal the strategy used by coal tits in assessing each other's fighting ability.

This study has given rise to a particularly interesting point : there is no indication that drift is related to the singing performance in coal tits, and thus that it was responsible for the evolution of song repertoires in this species.

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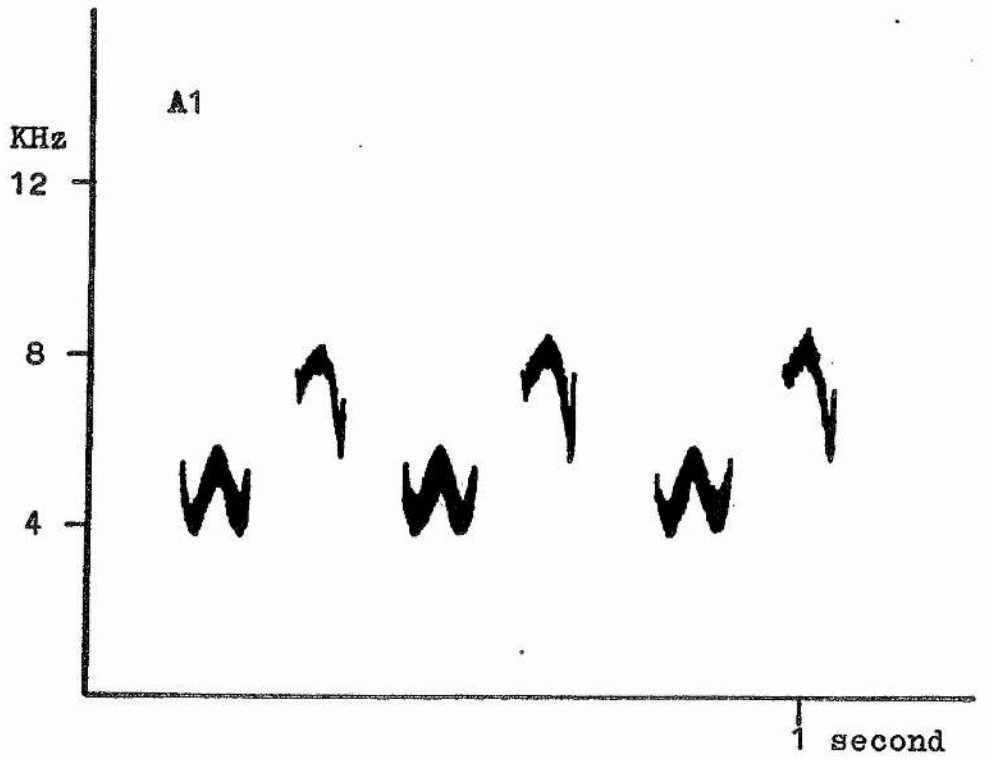
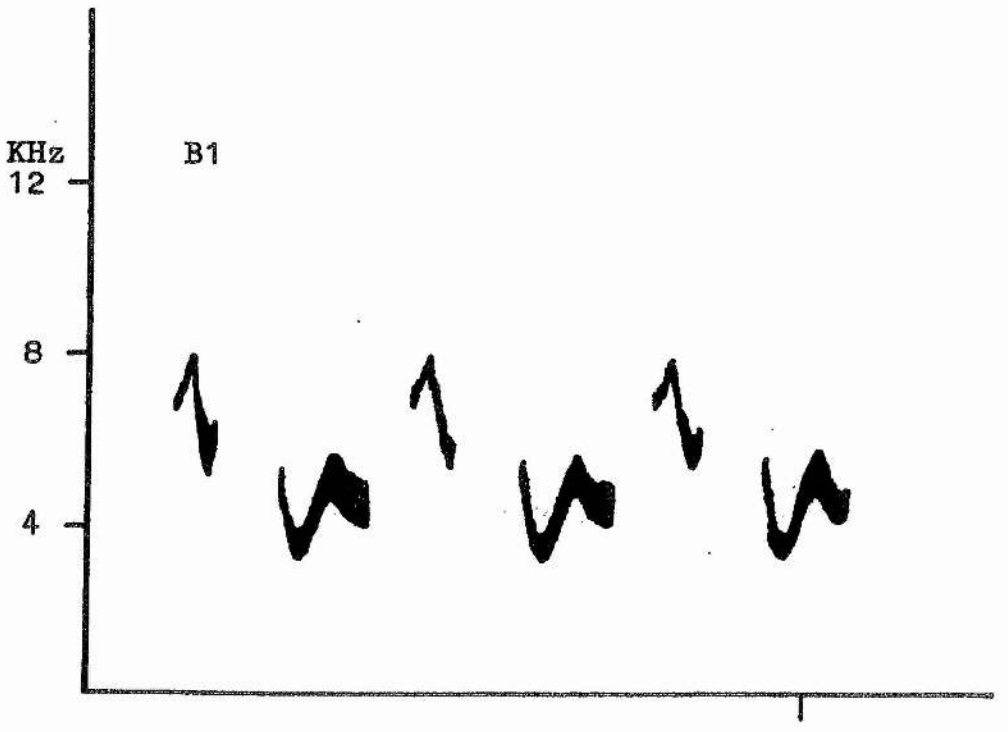
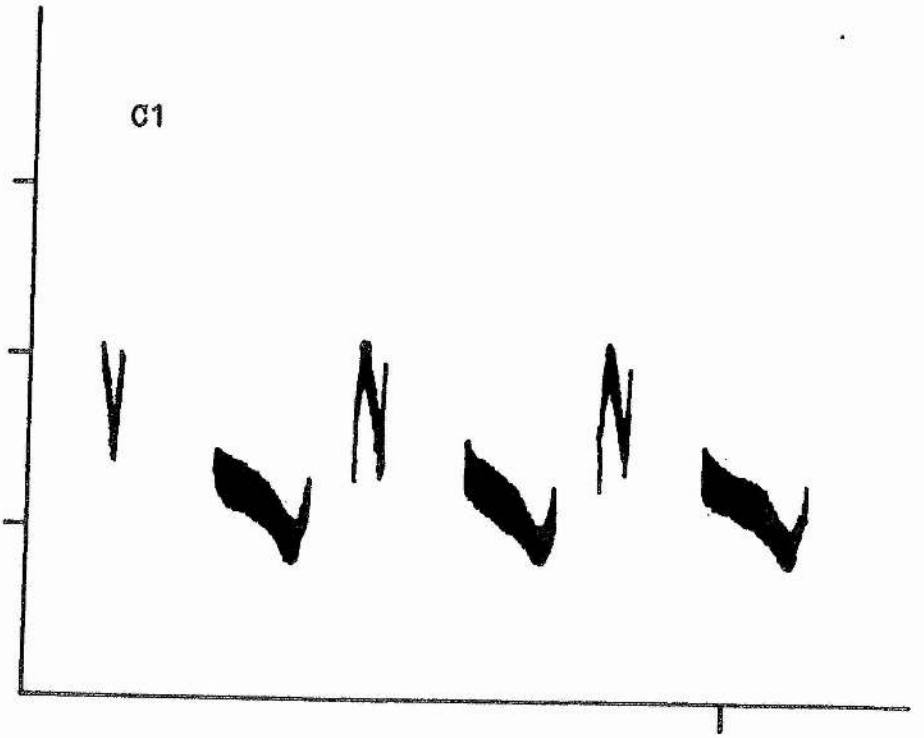
Appendix 1.1. Sonagrams of song types recorded in Tentsmuir and at Loch Garten.


A1
KHz
12
8
4
1 second


KHz
12
B1
8
4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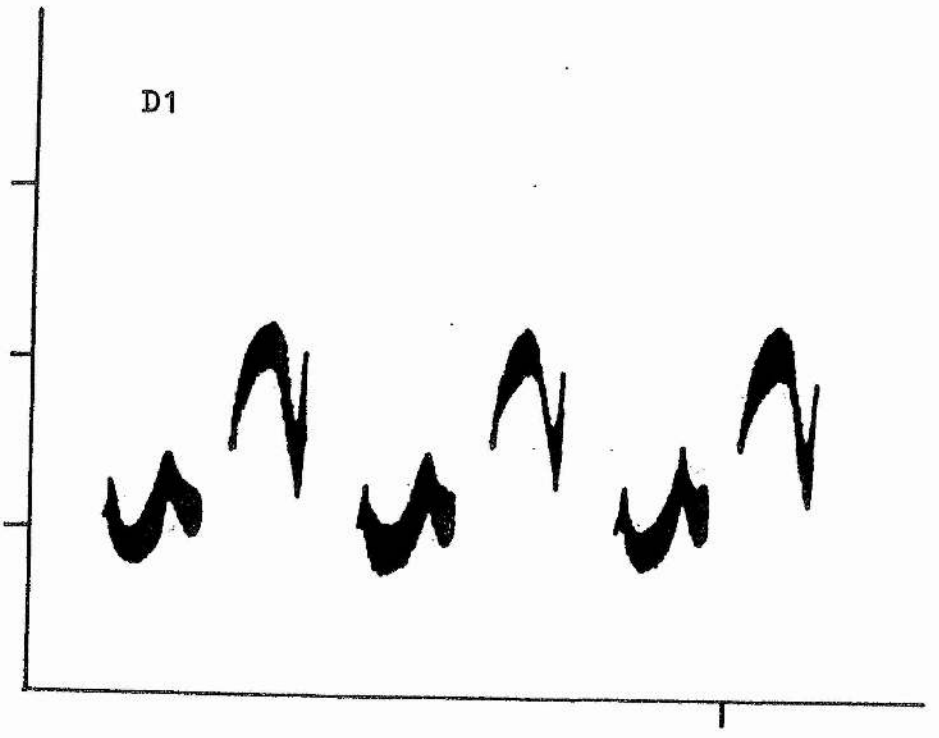
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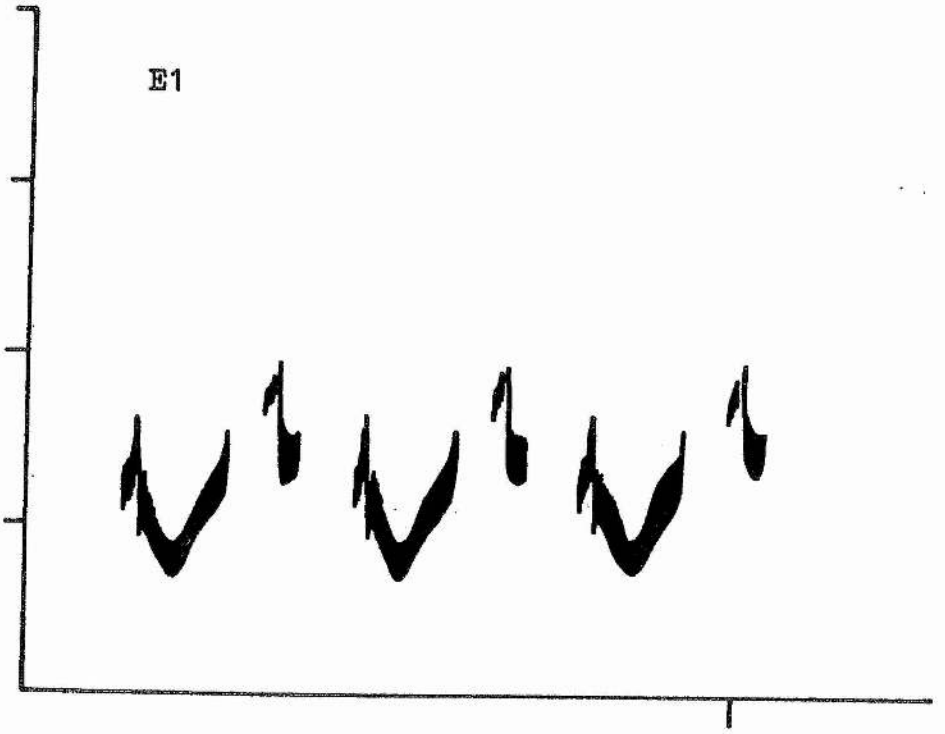
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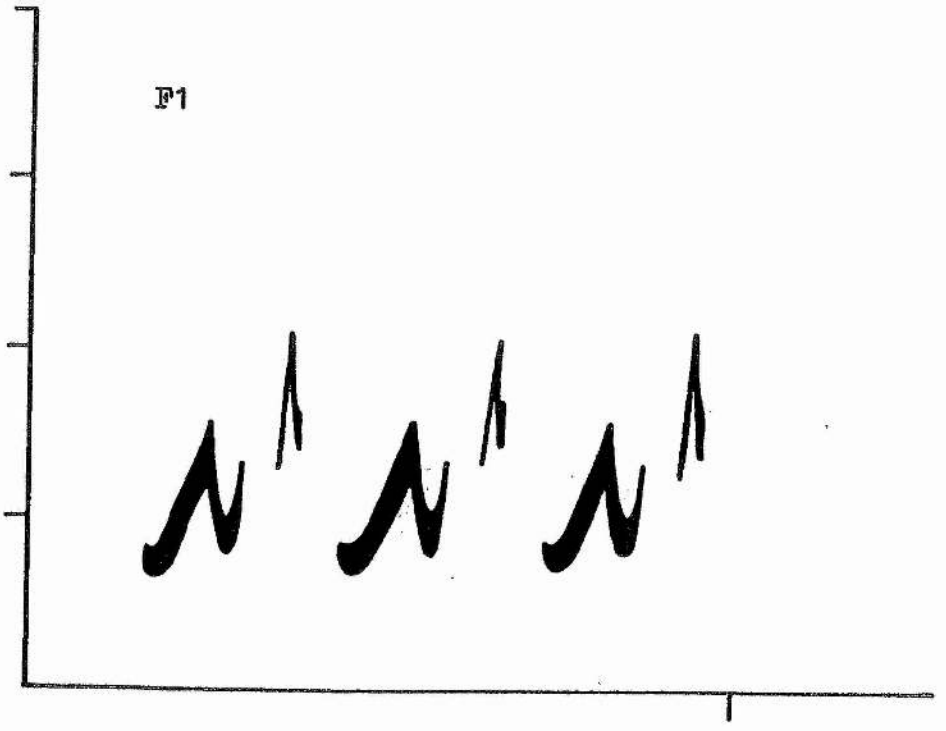
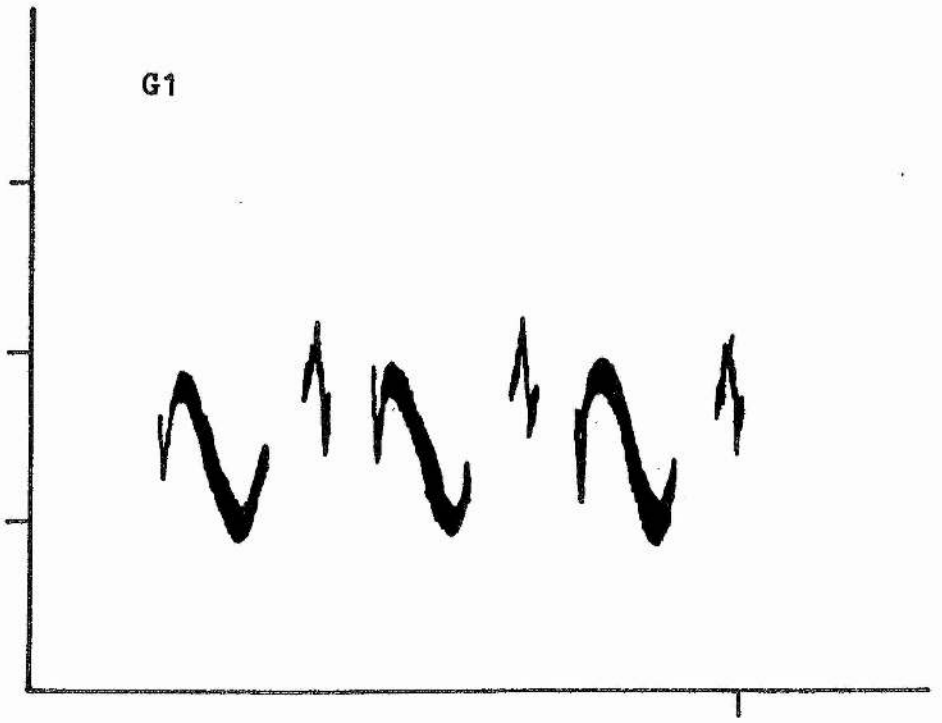

F1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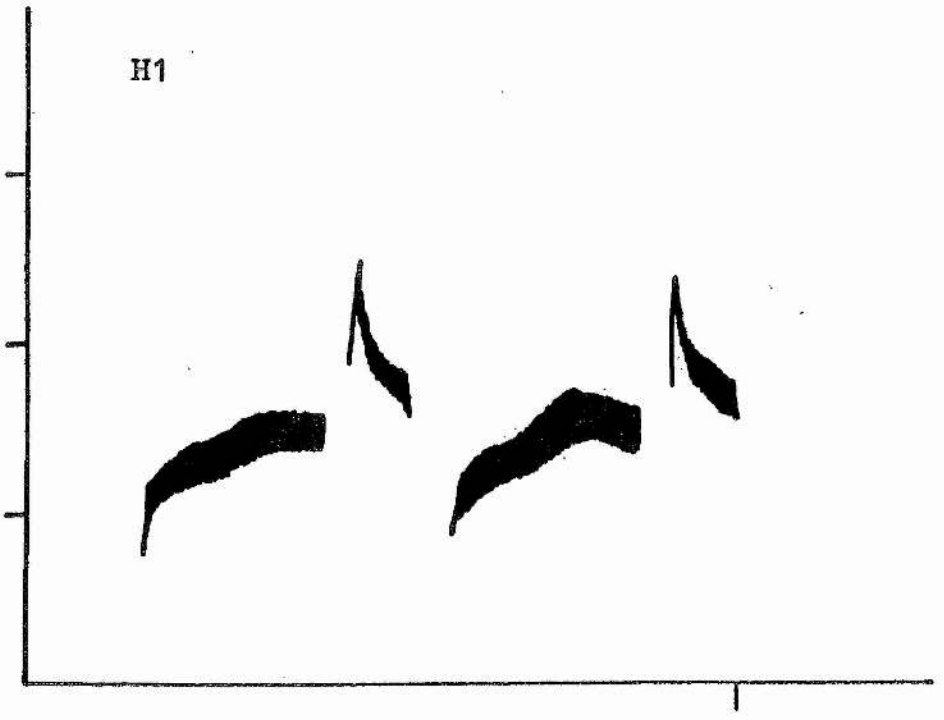
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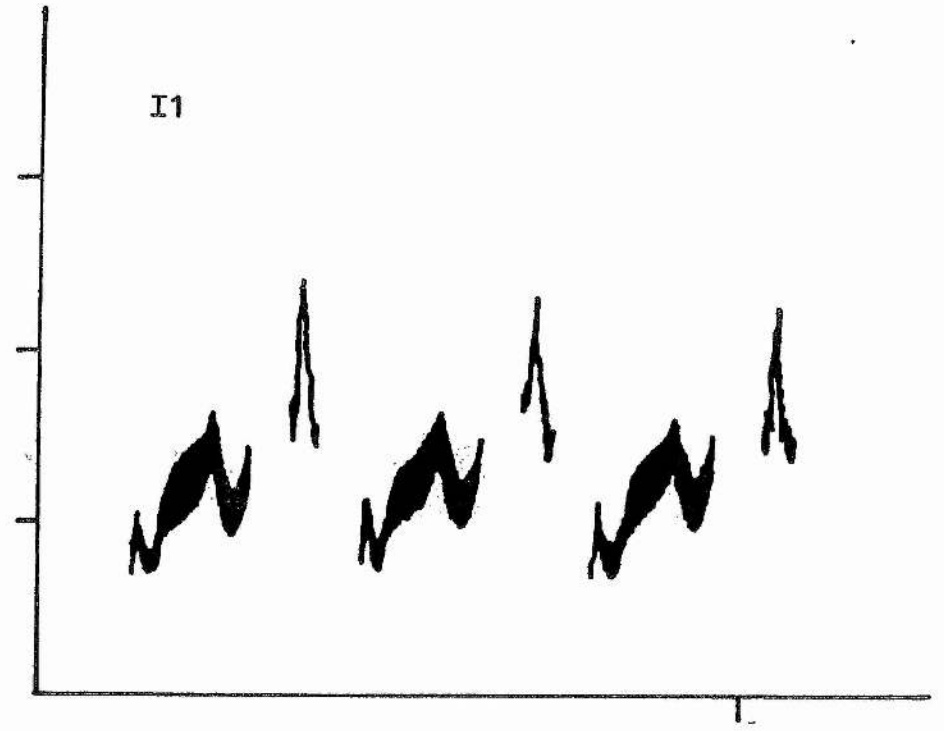
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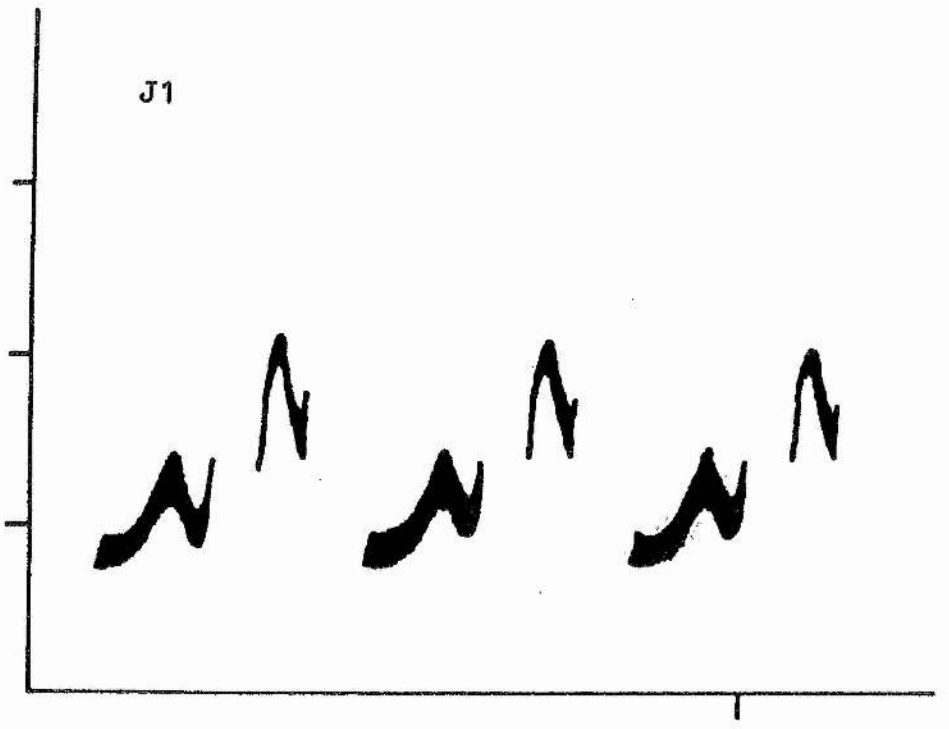
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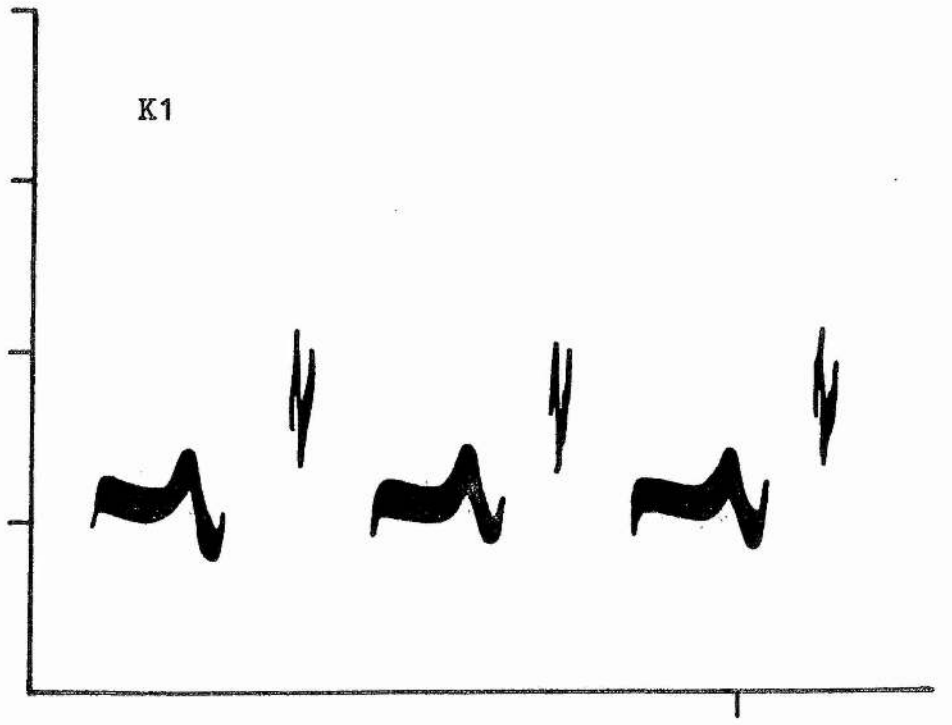
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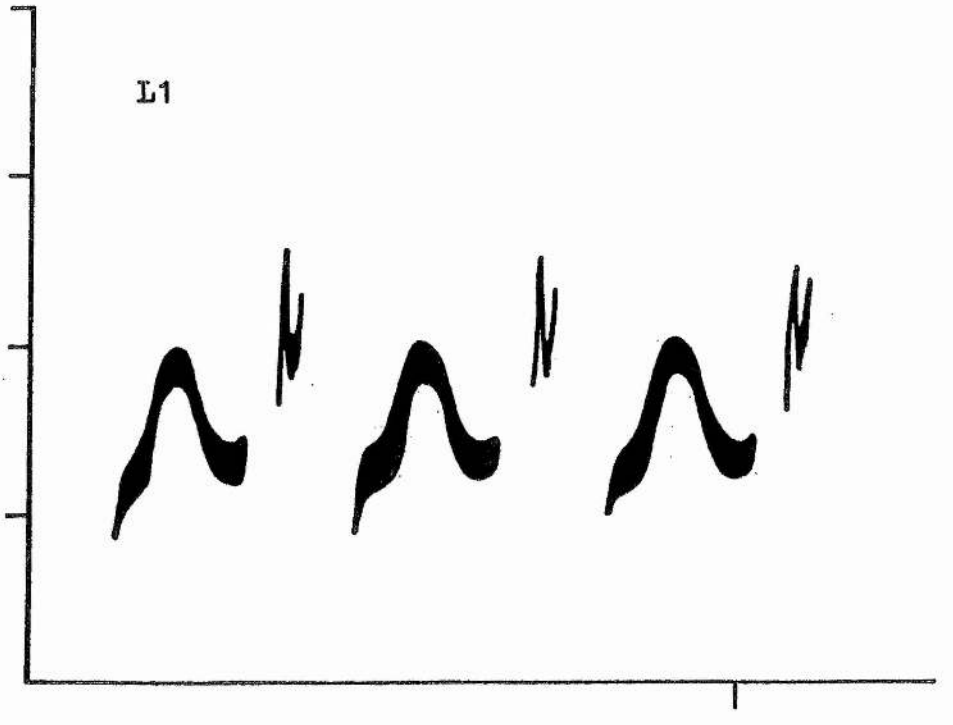
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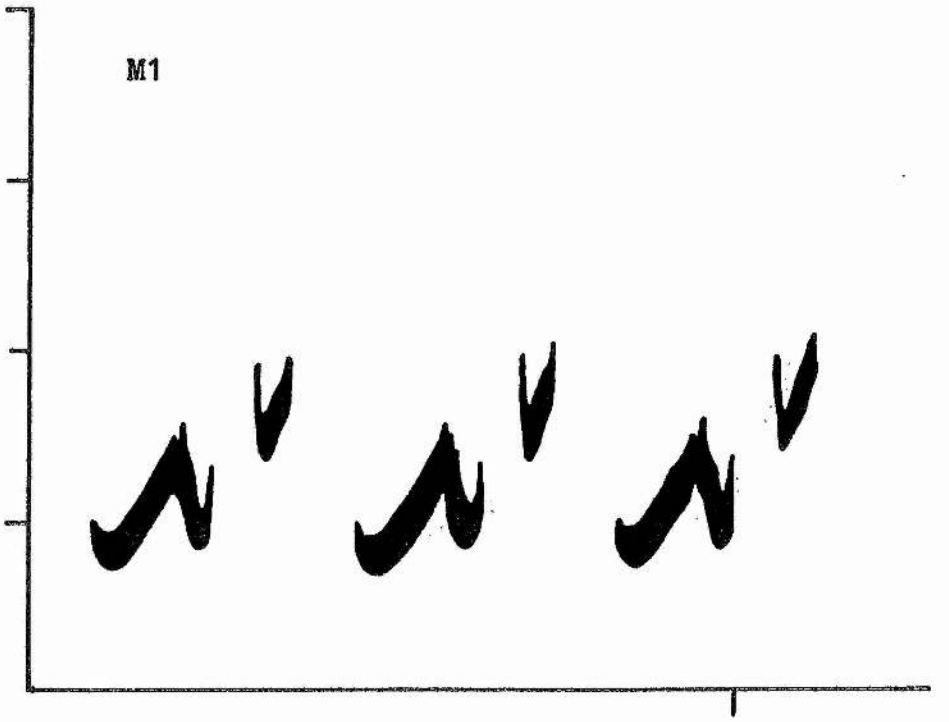
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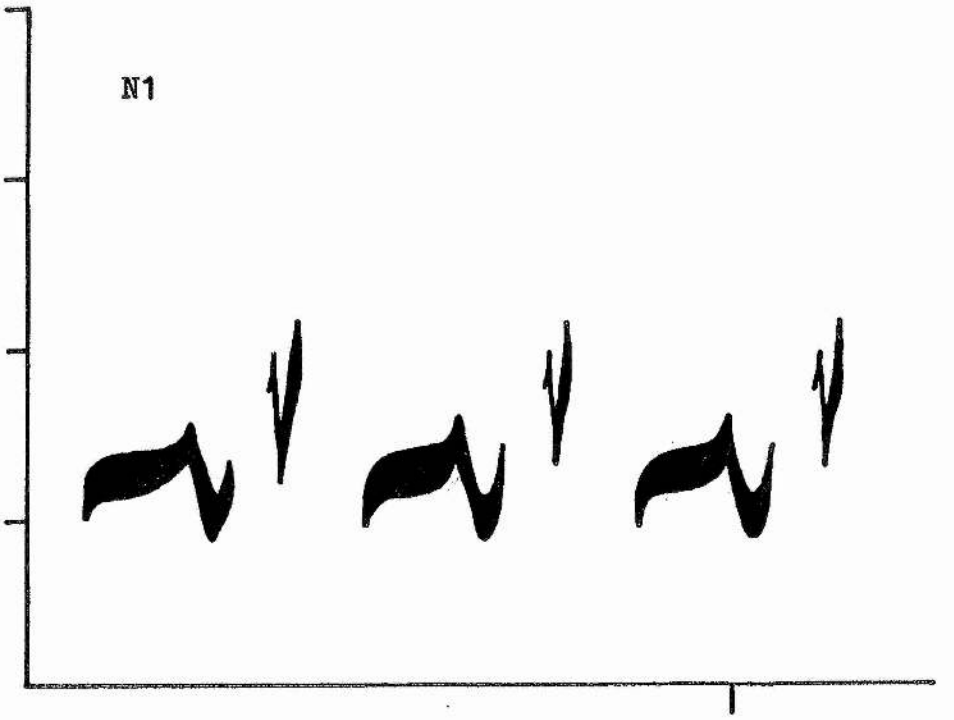
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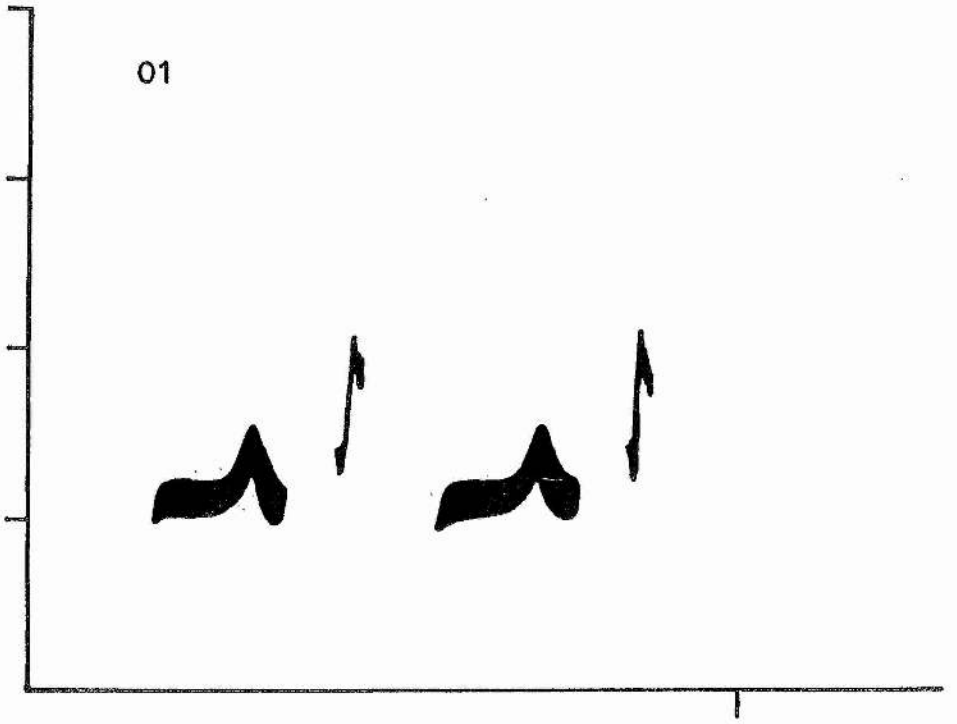
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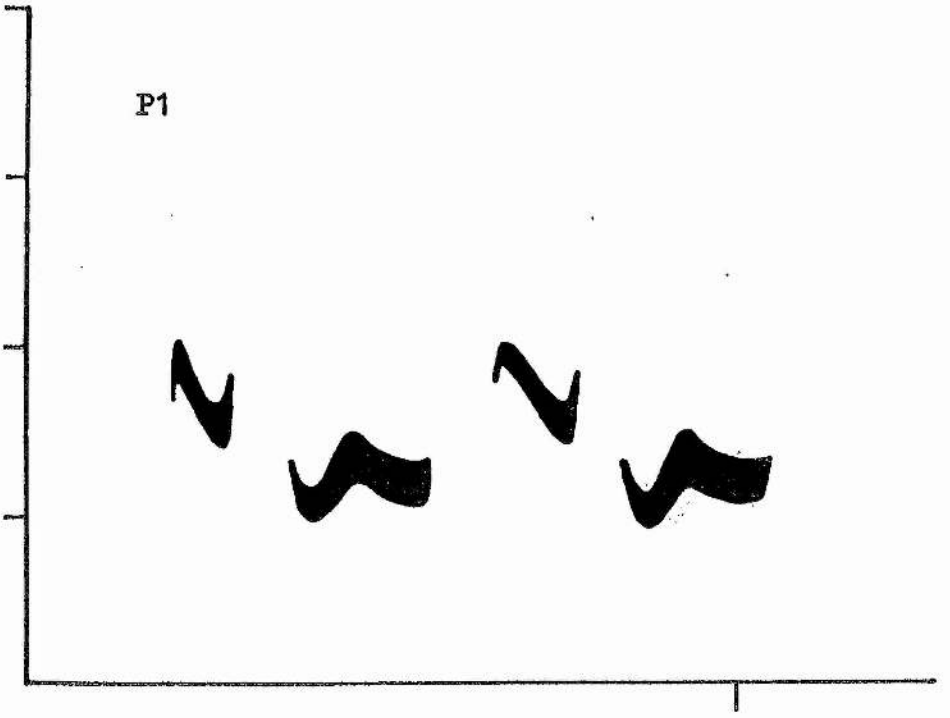
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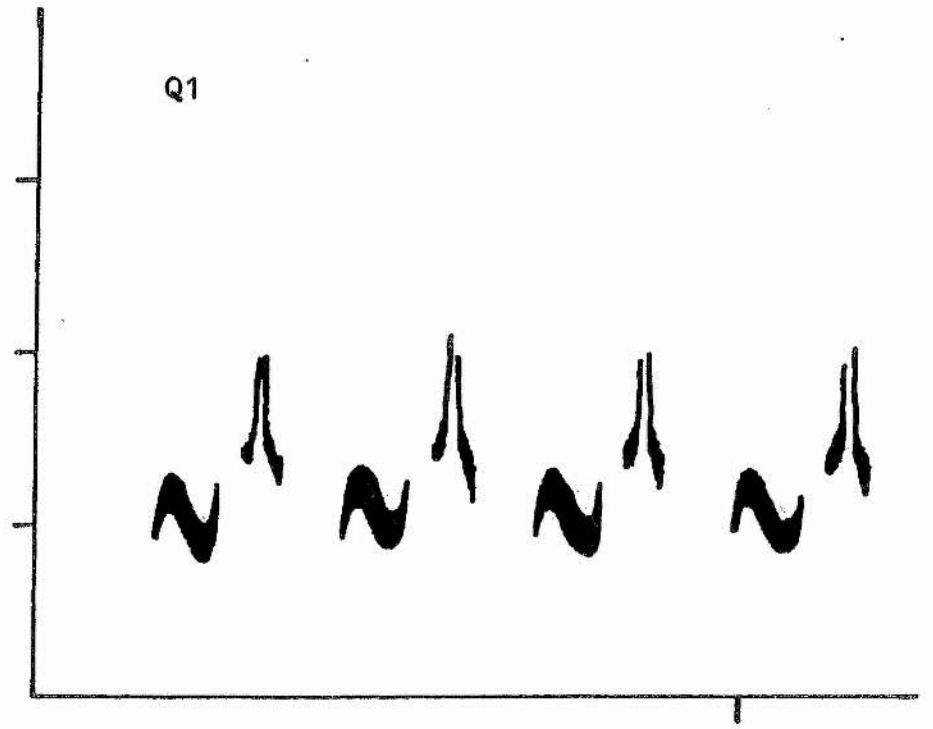
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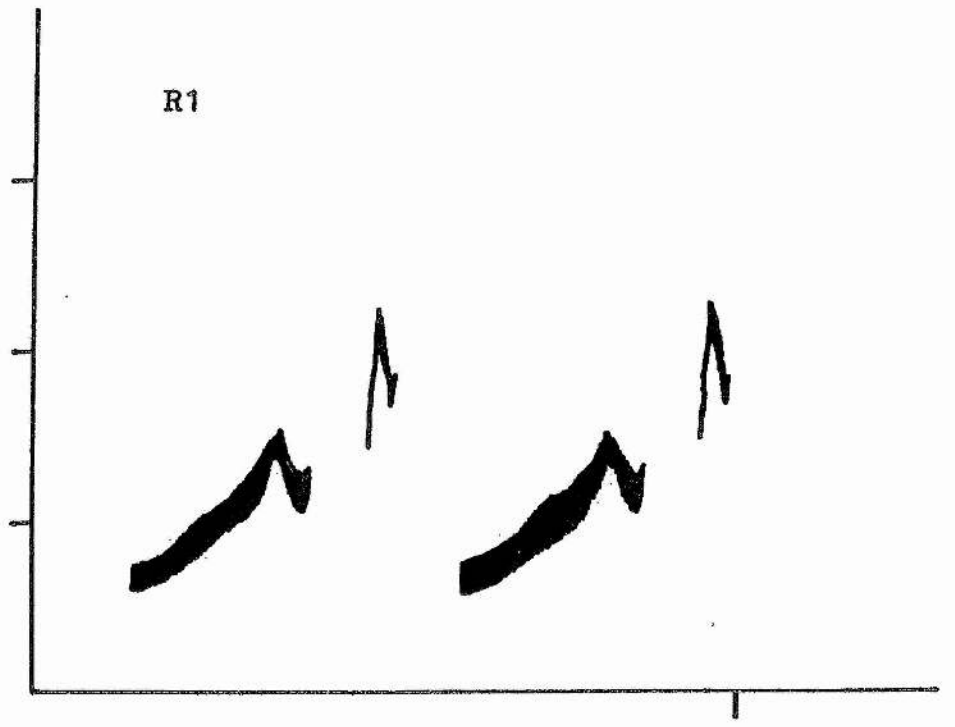
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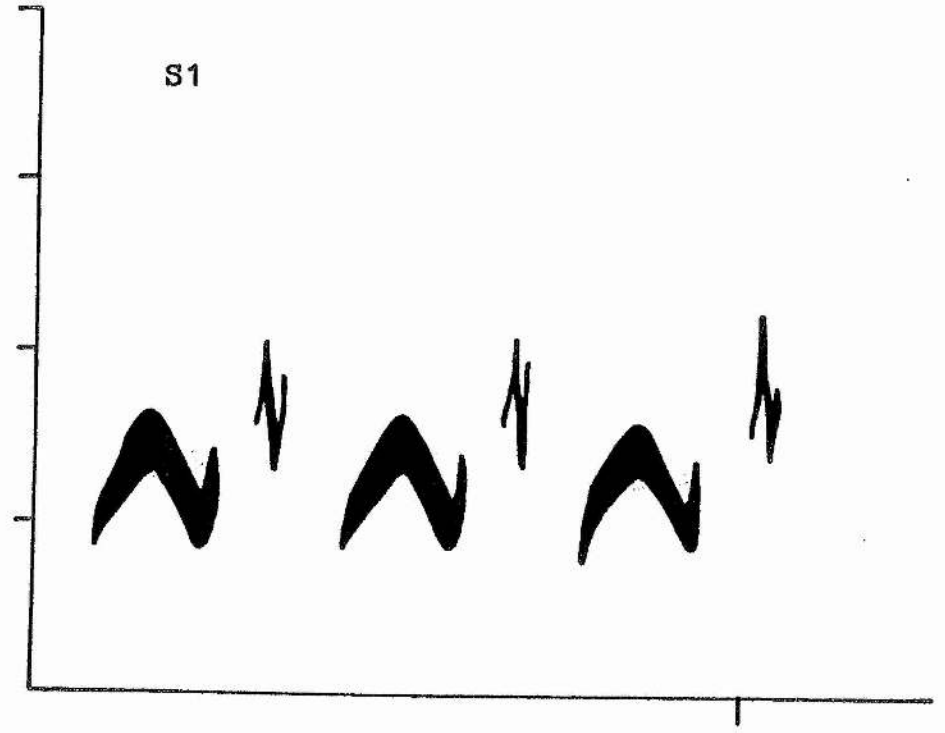
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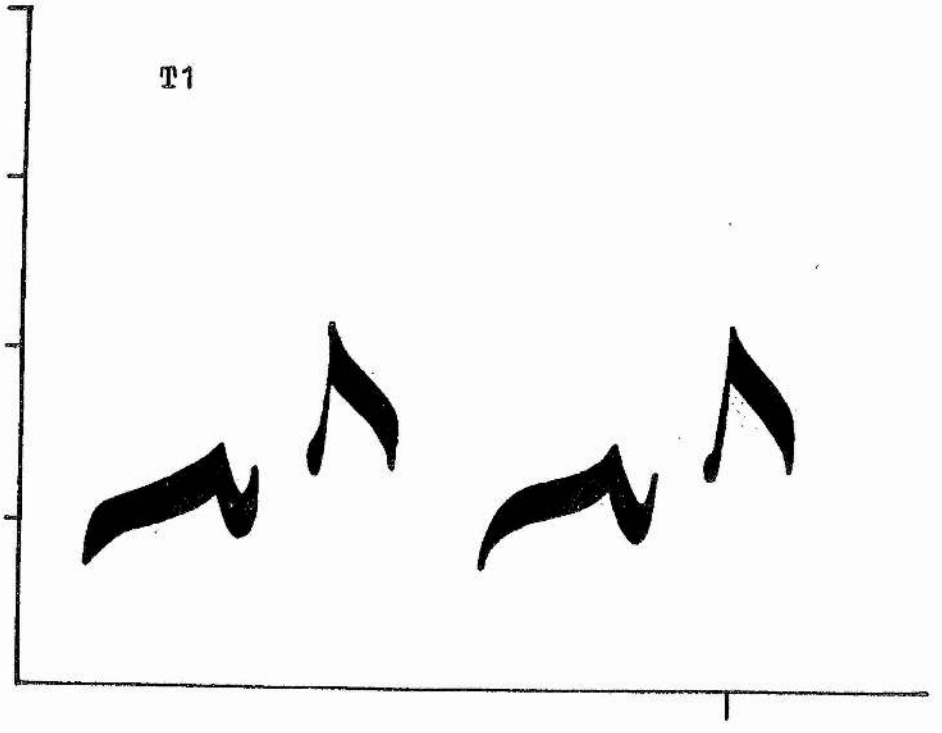
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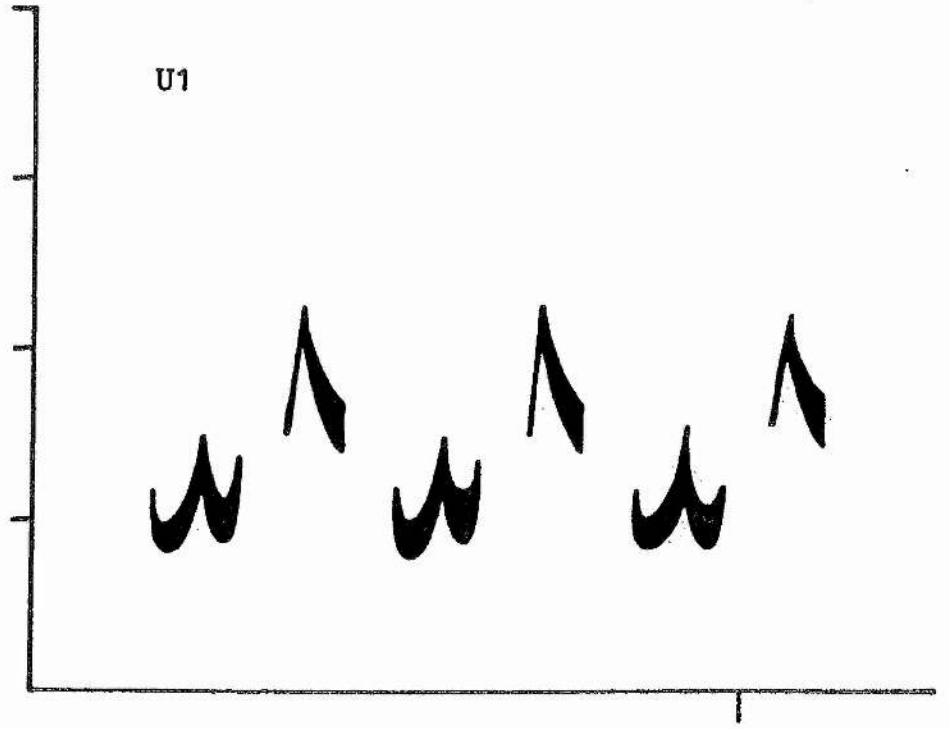
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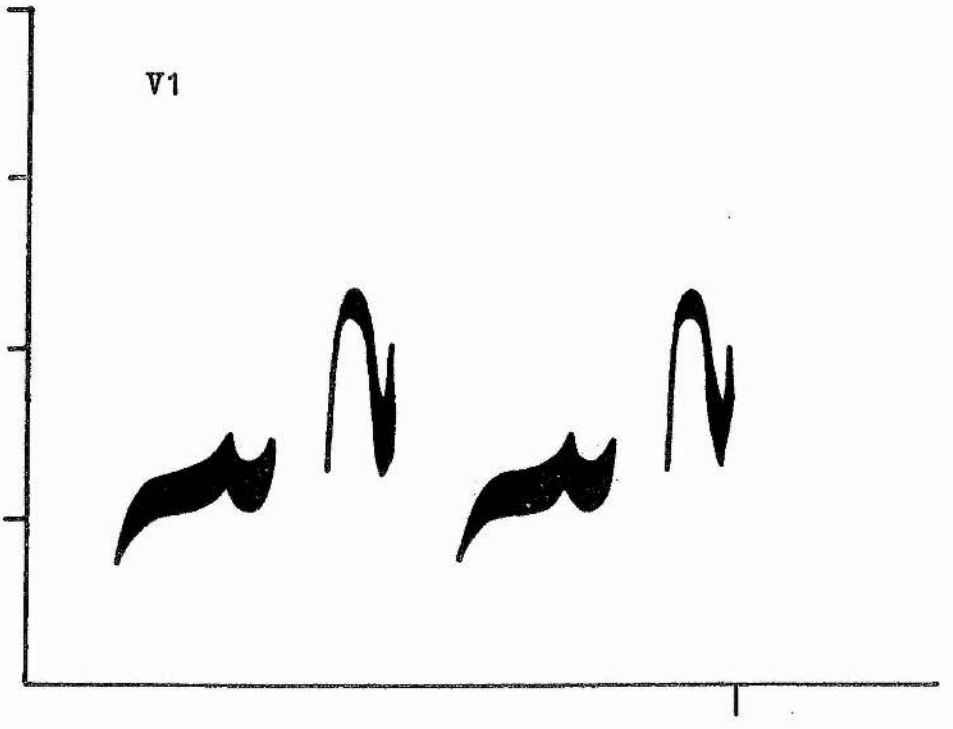
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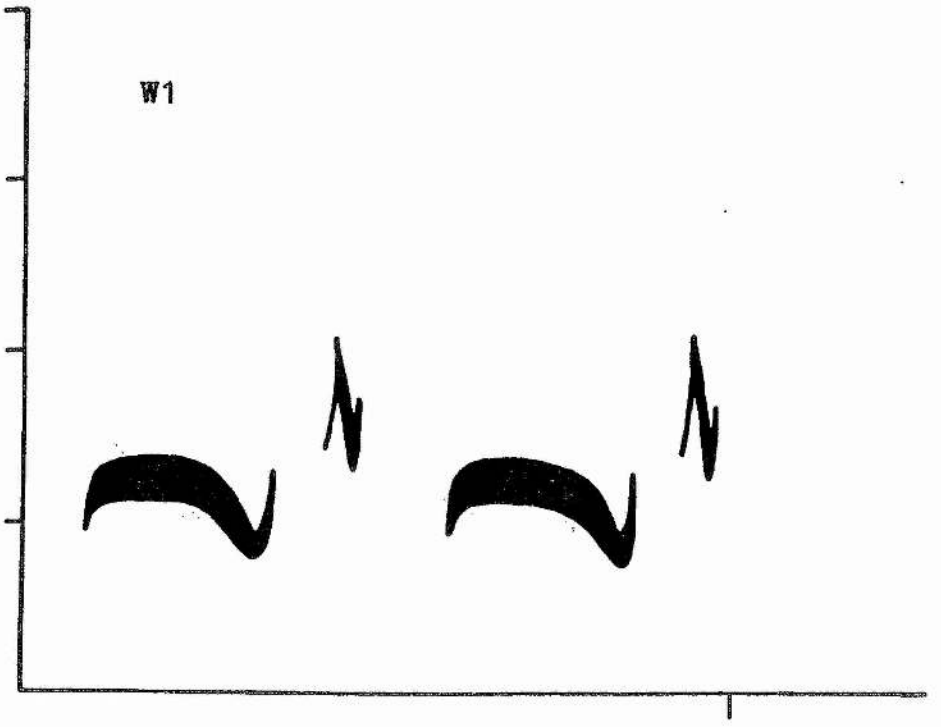
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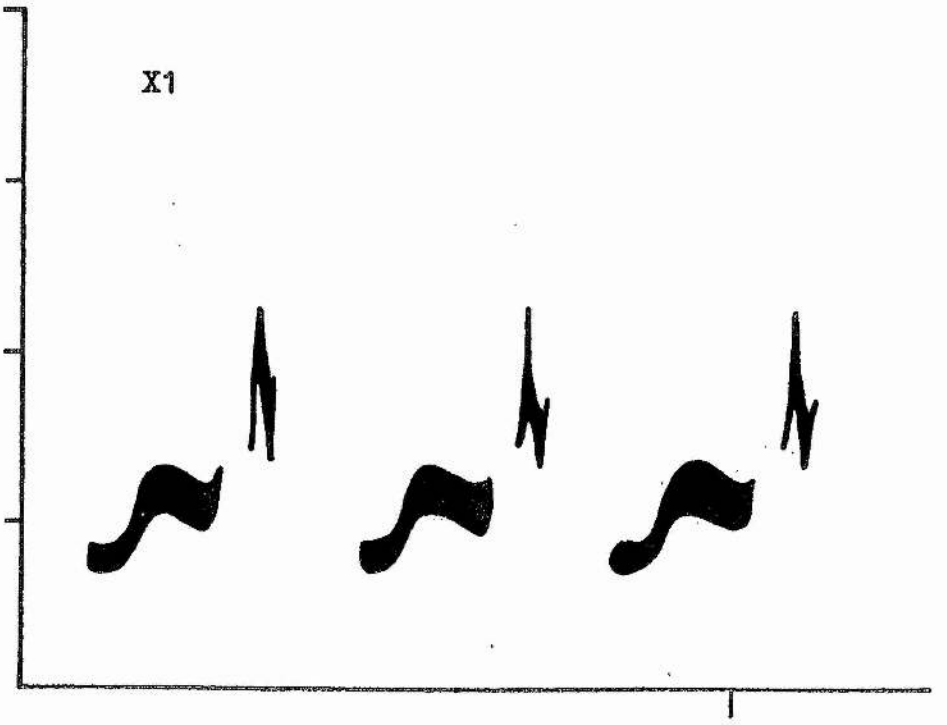
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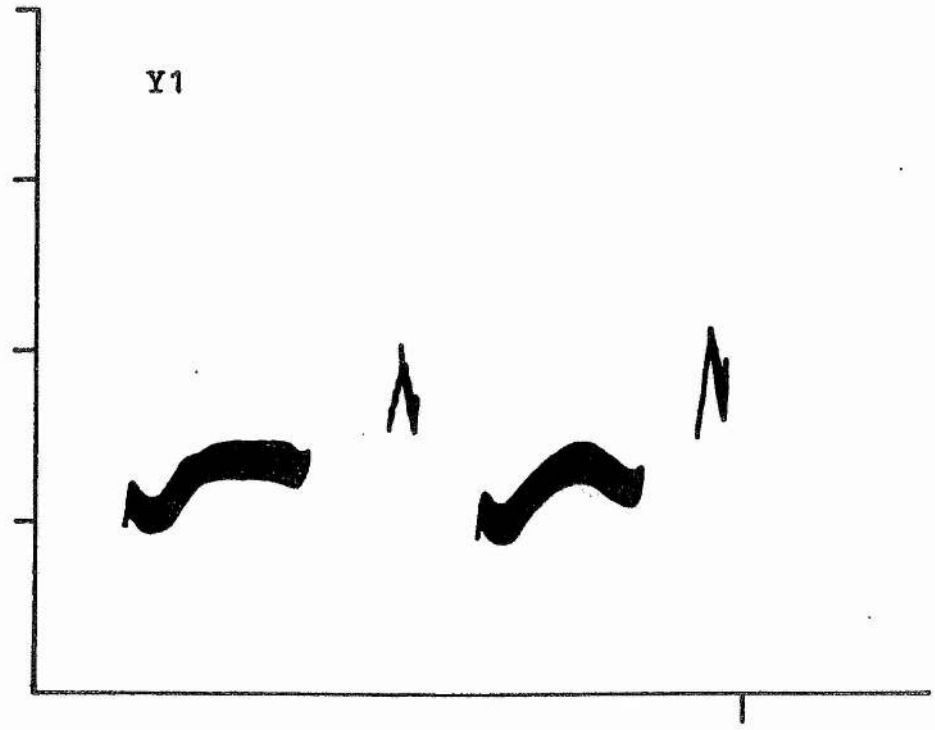
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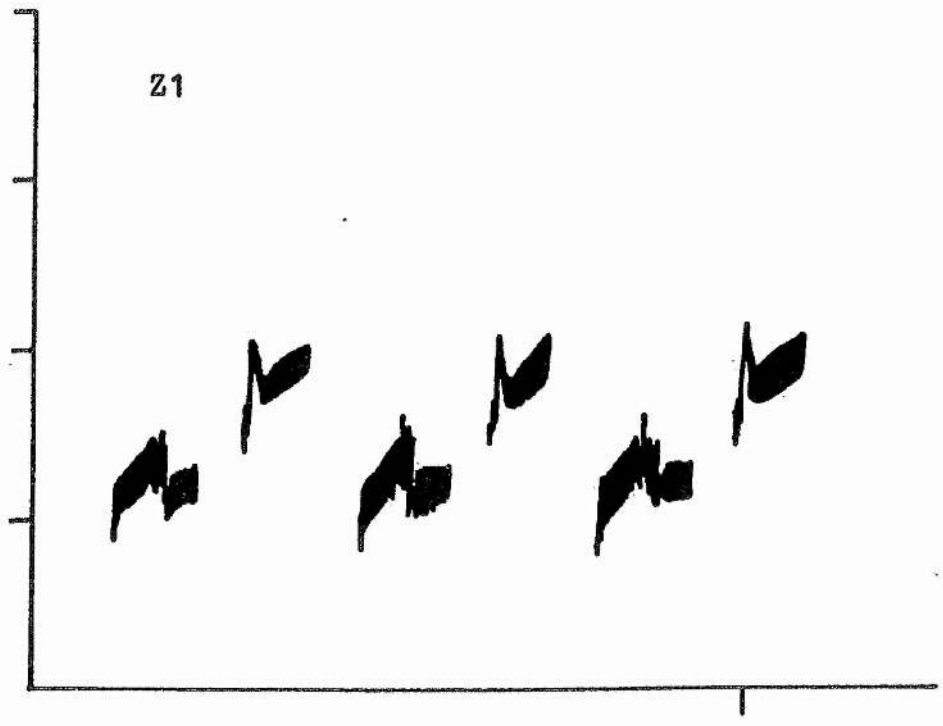
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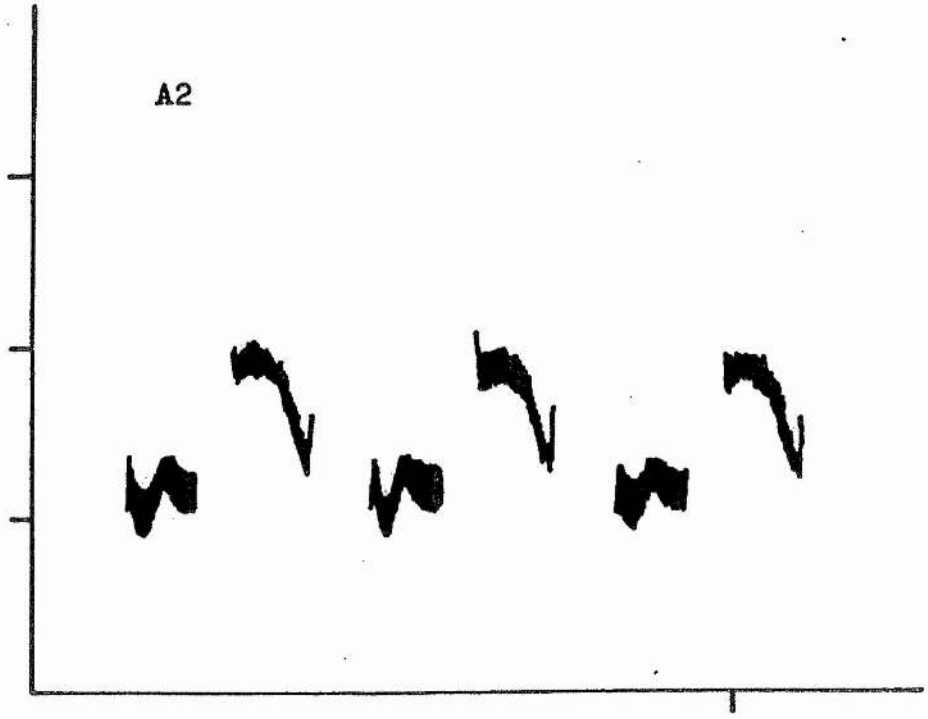
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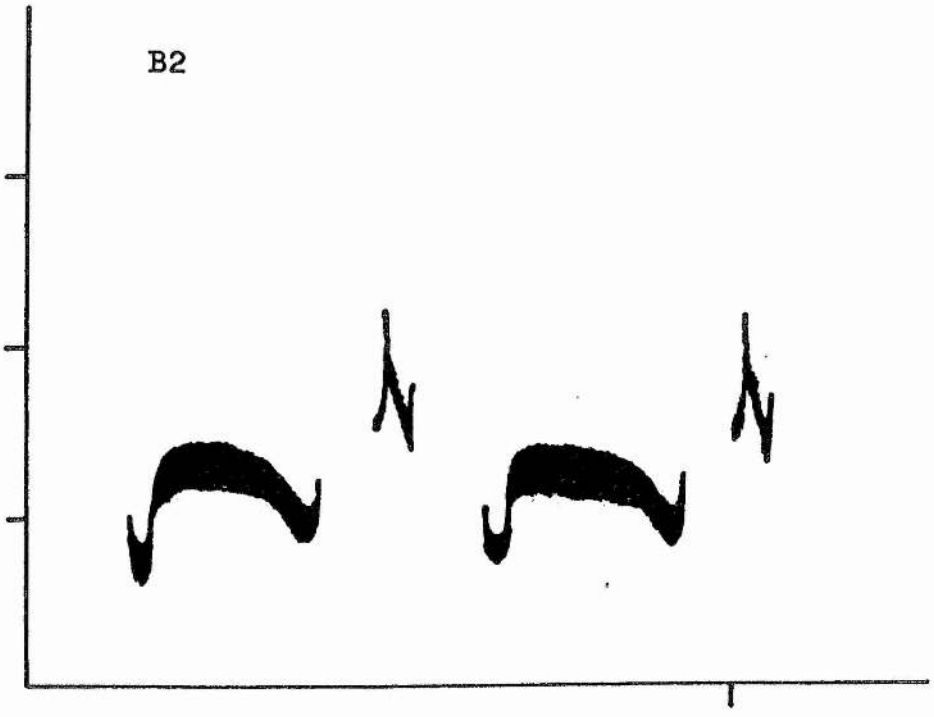
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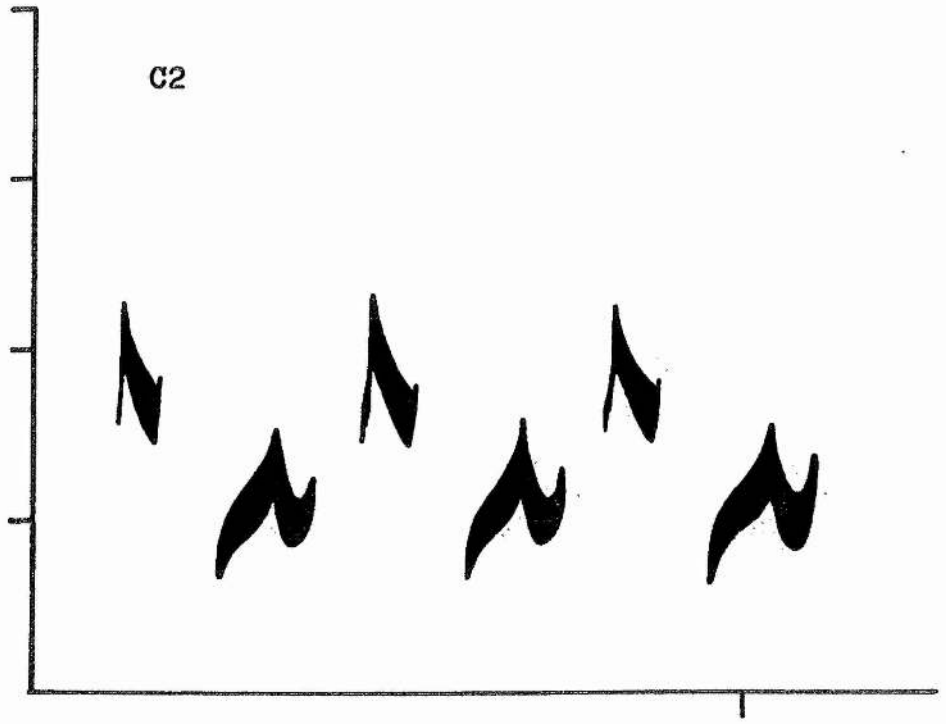
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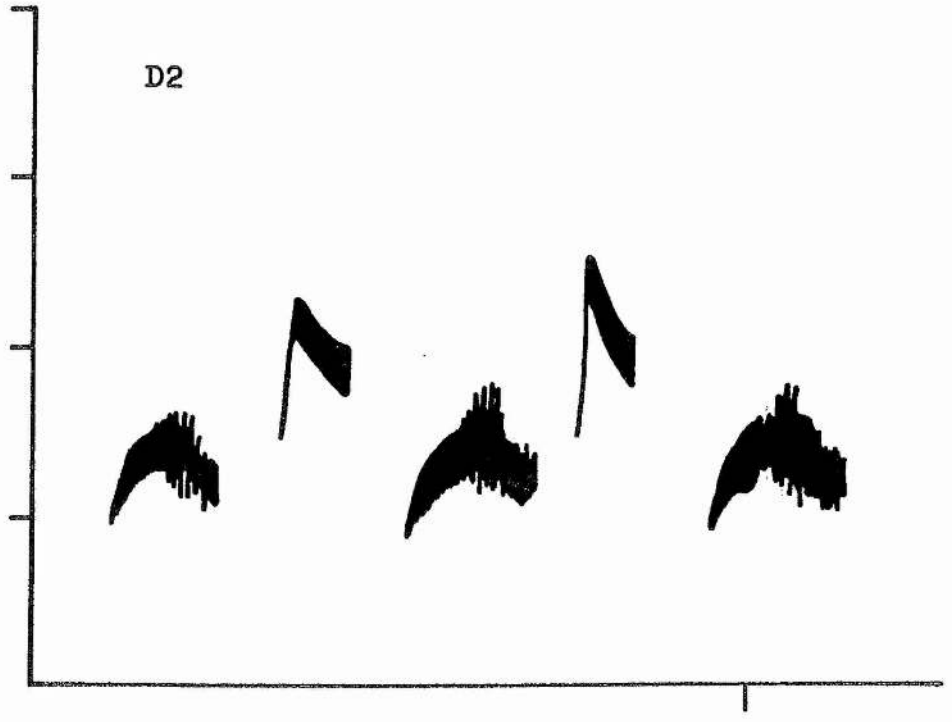
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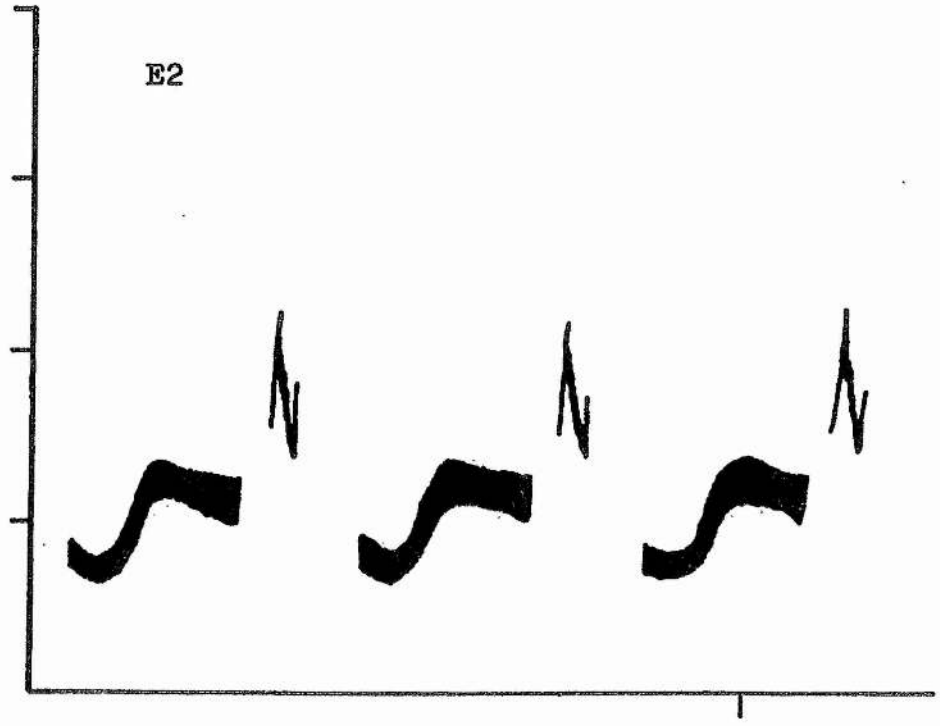
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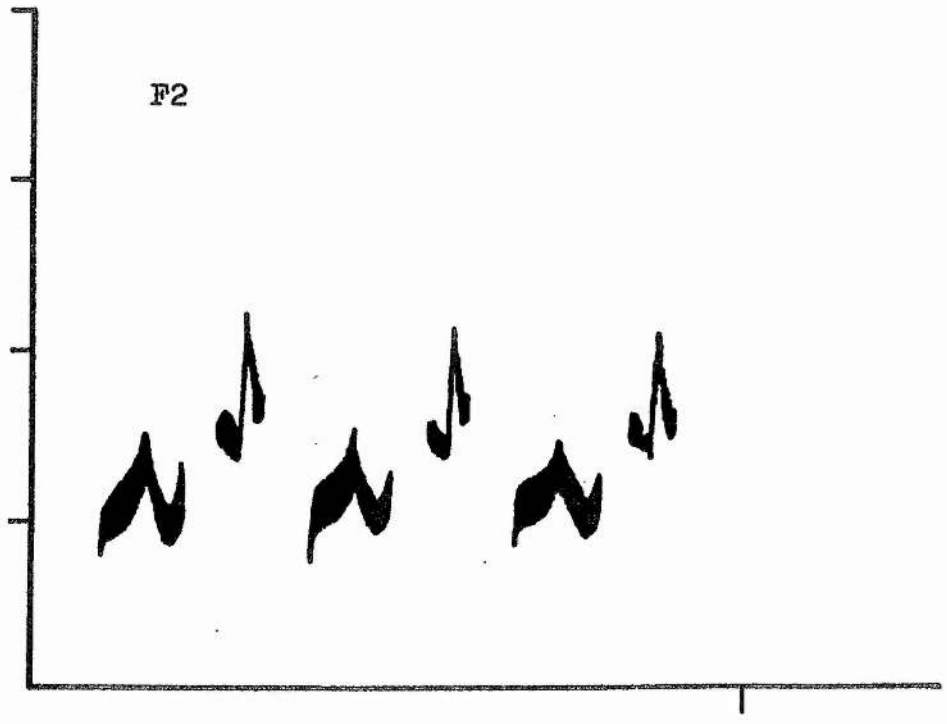
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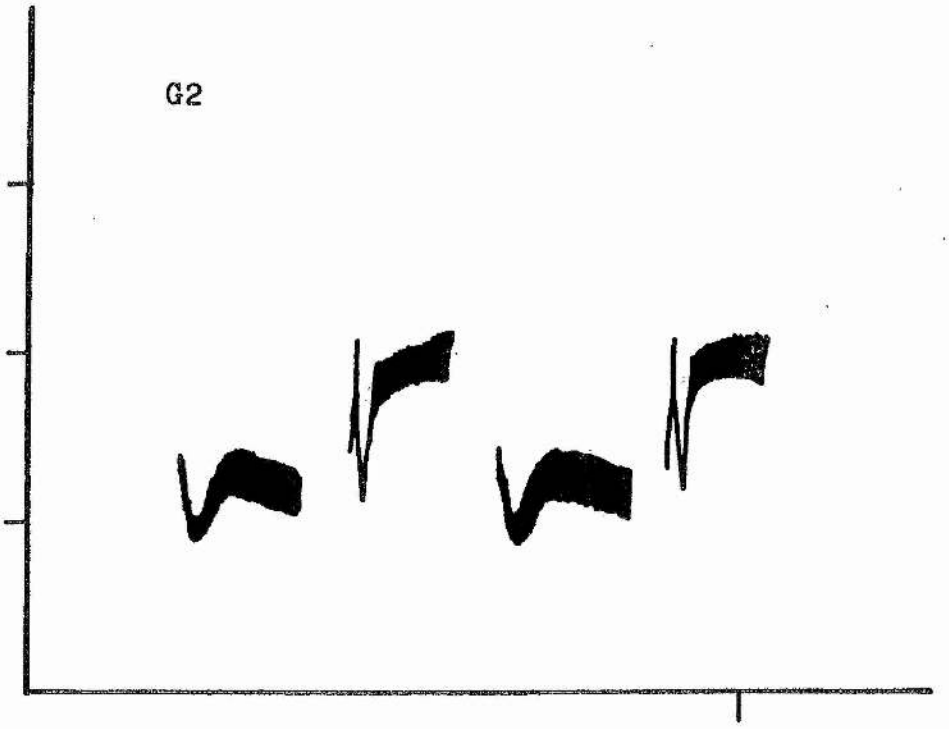
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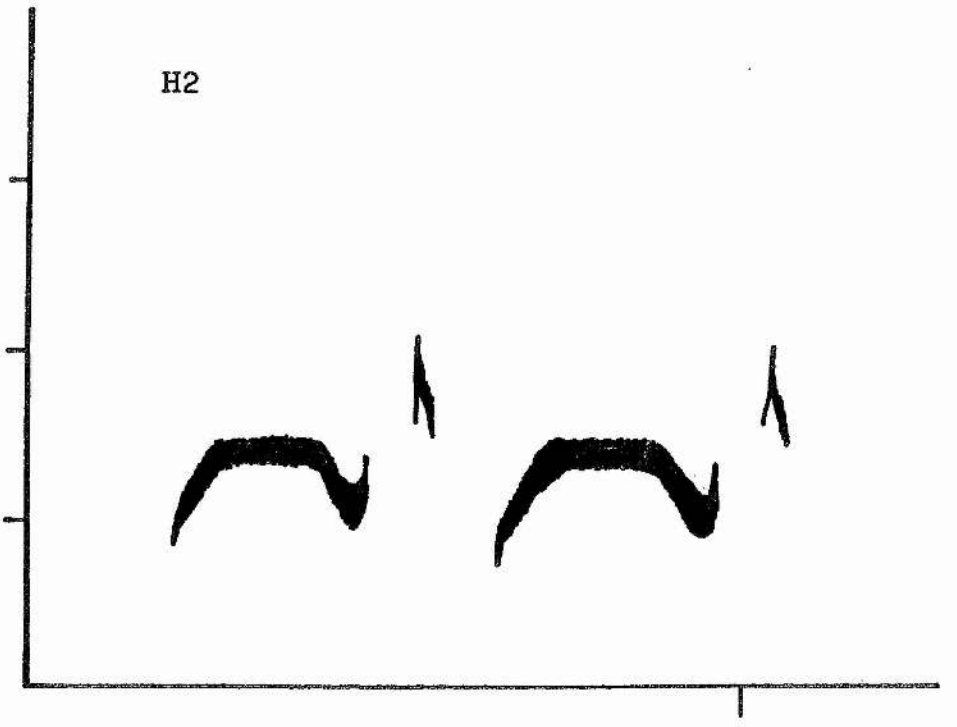
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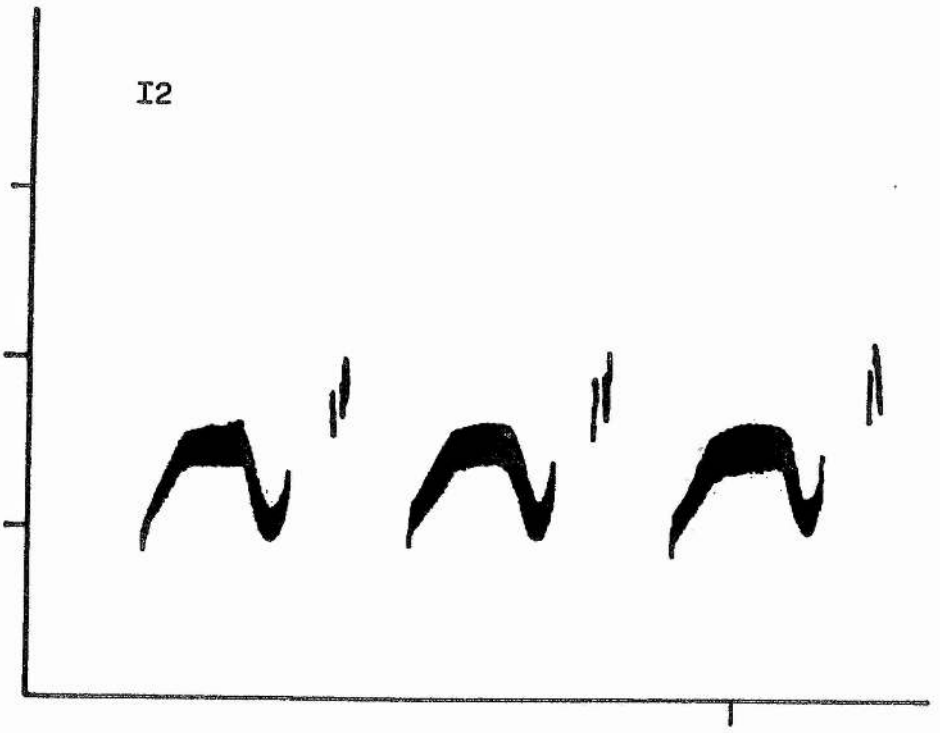
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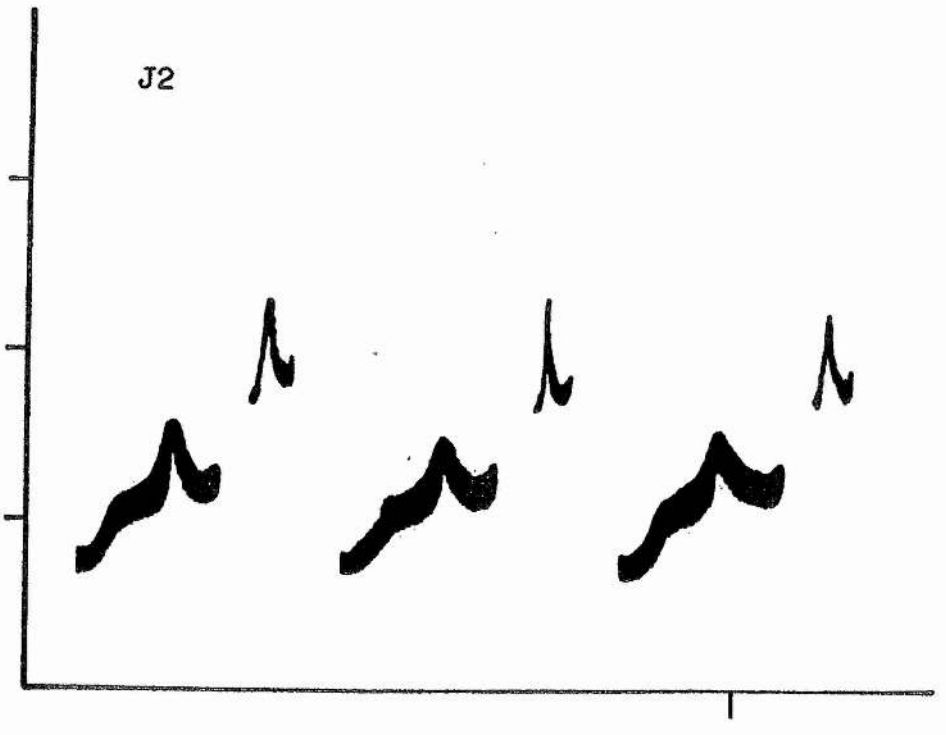
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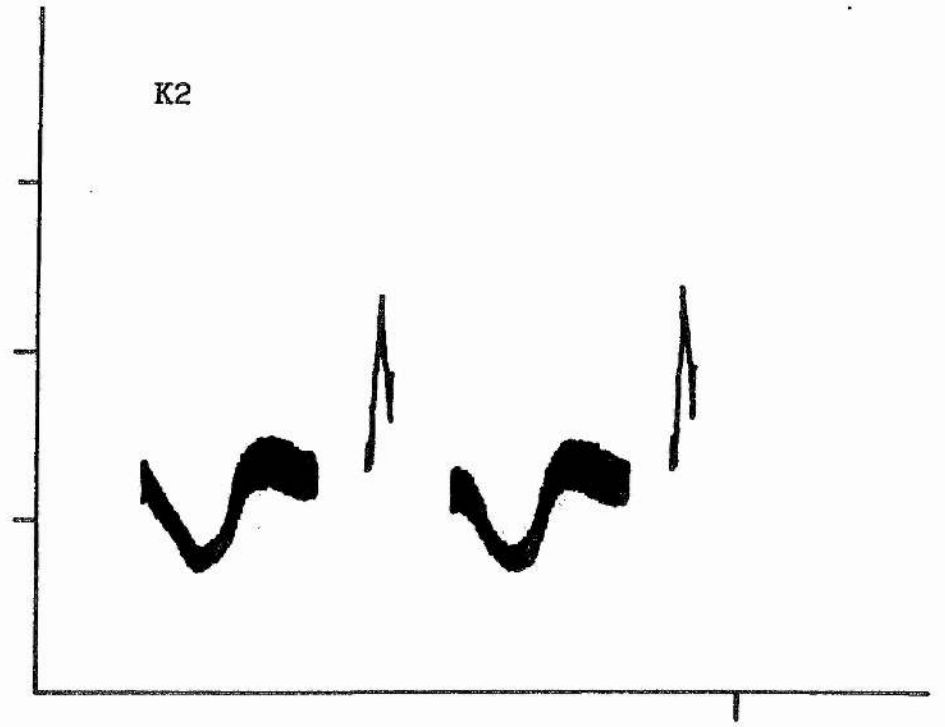
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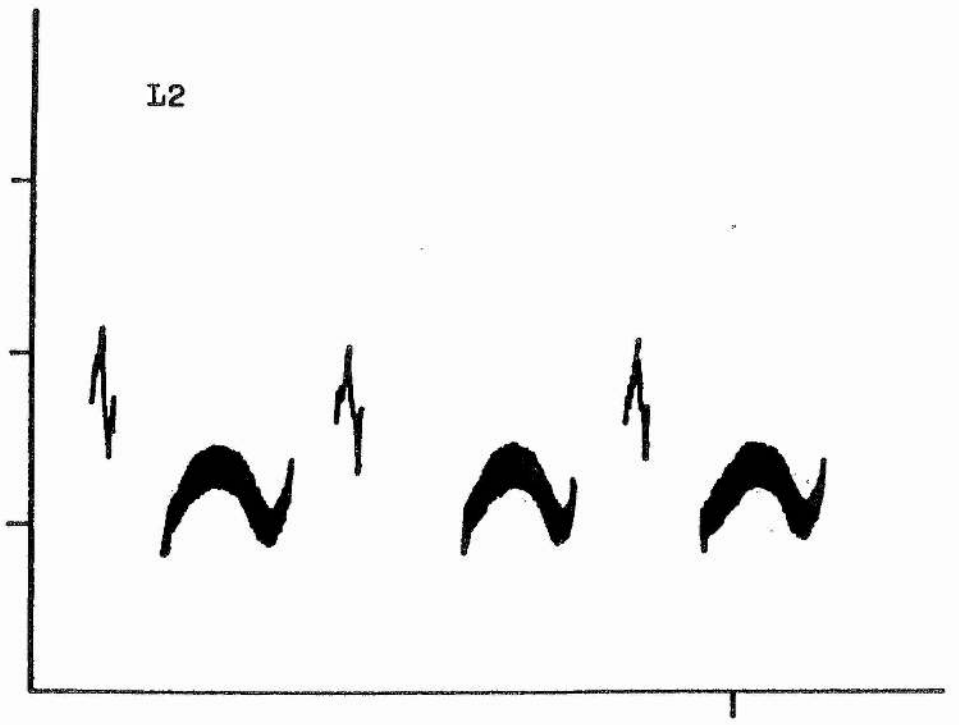
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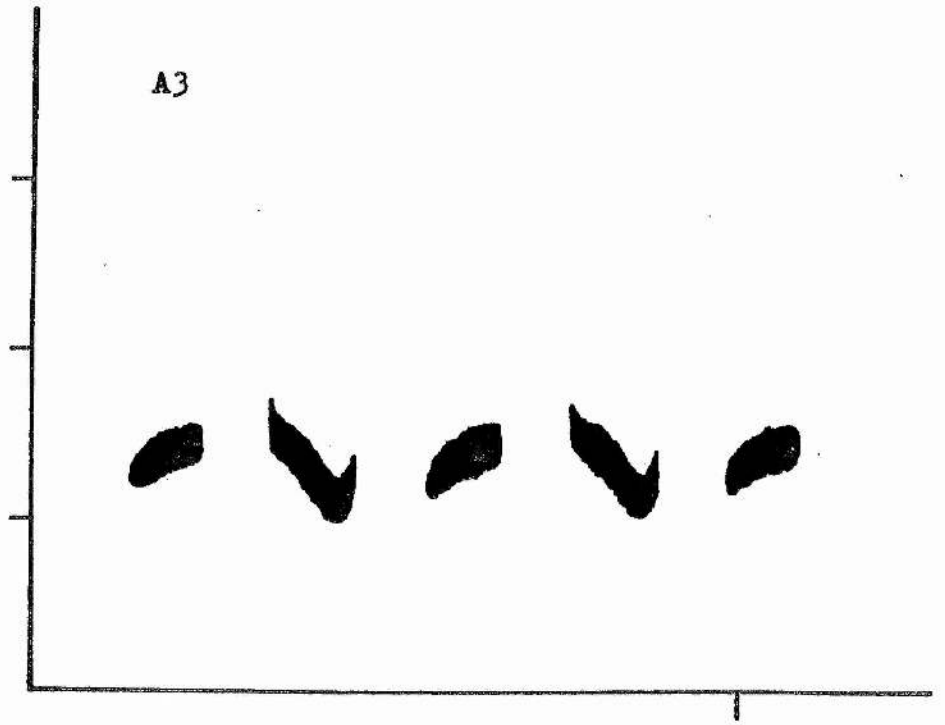
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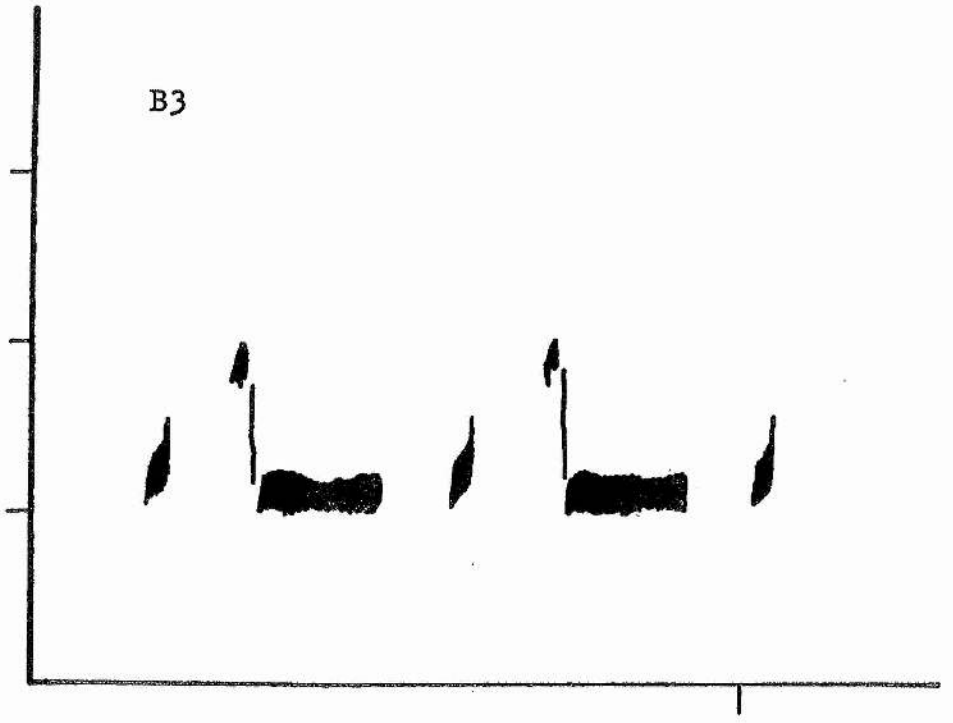
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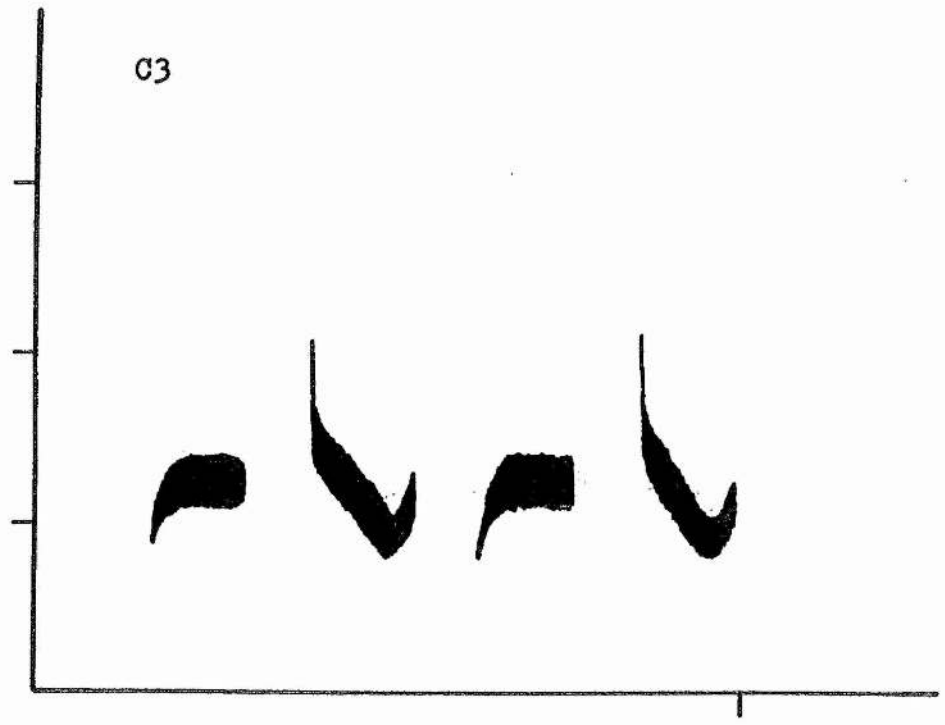
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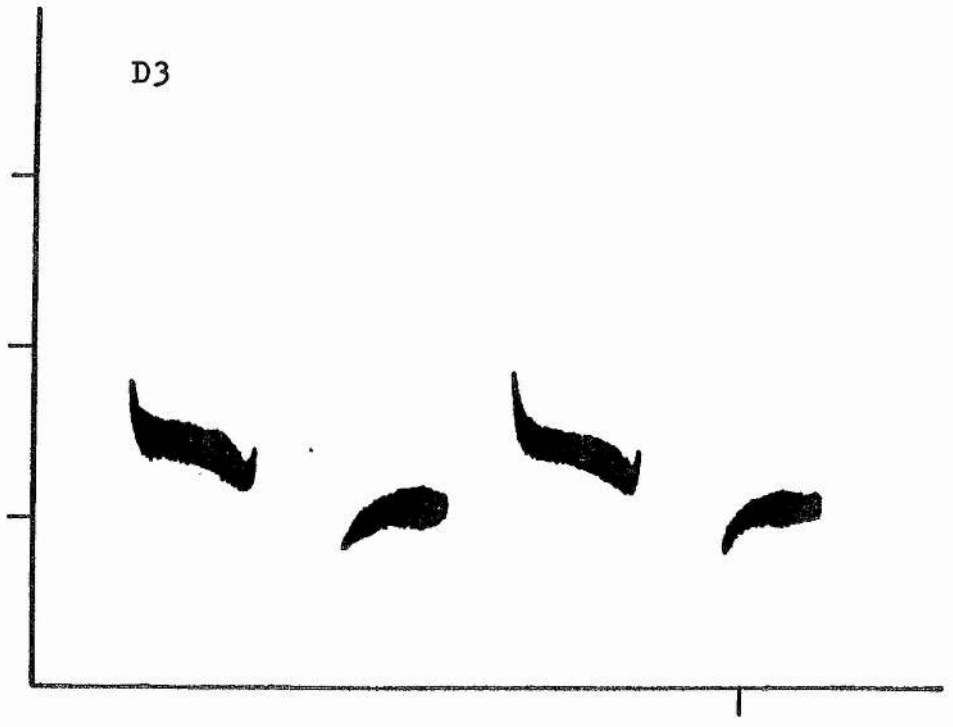
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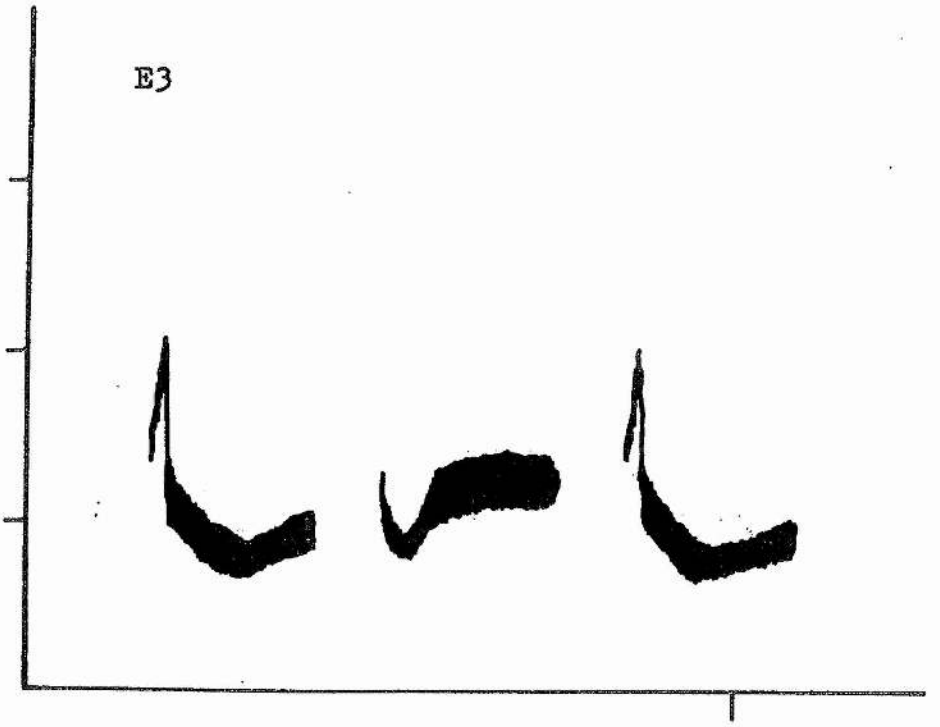
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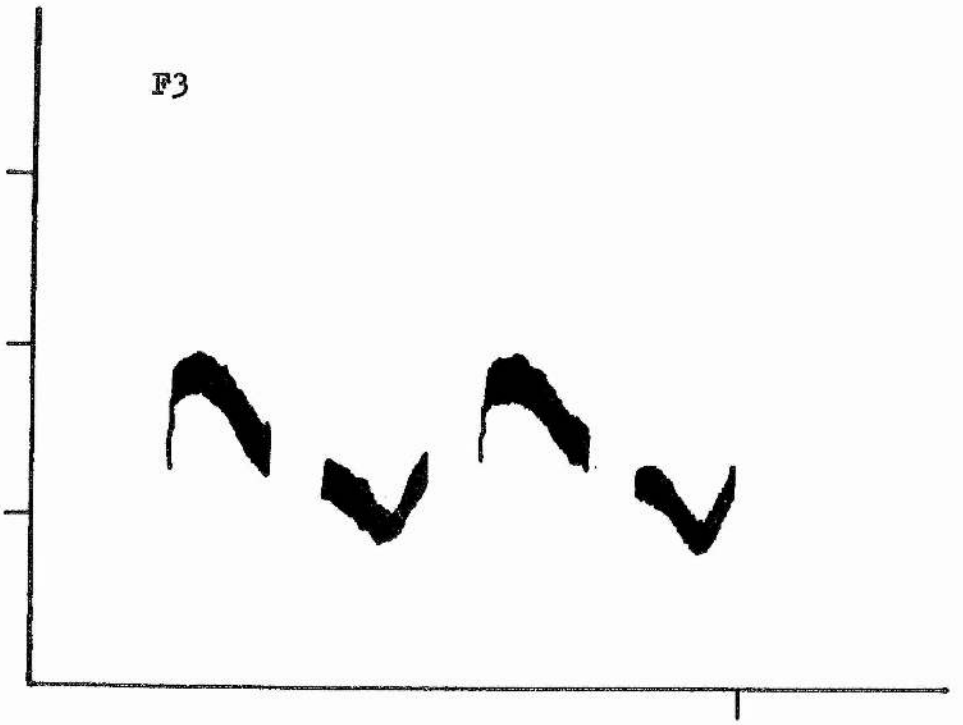
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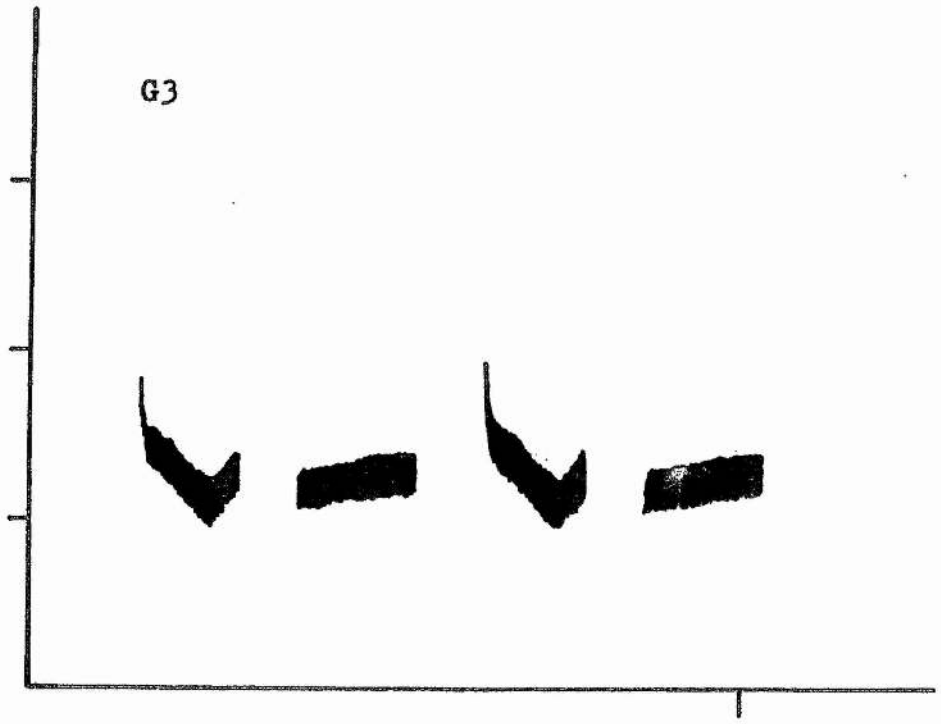
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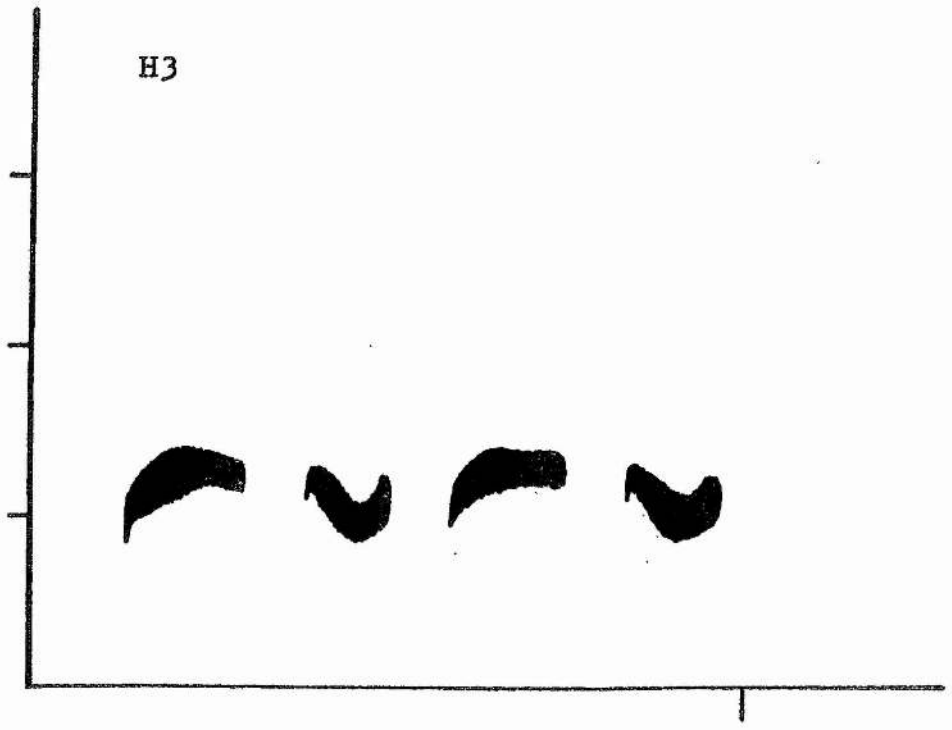
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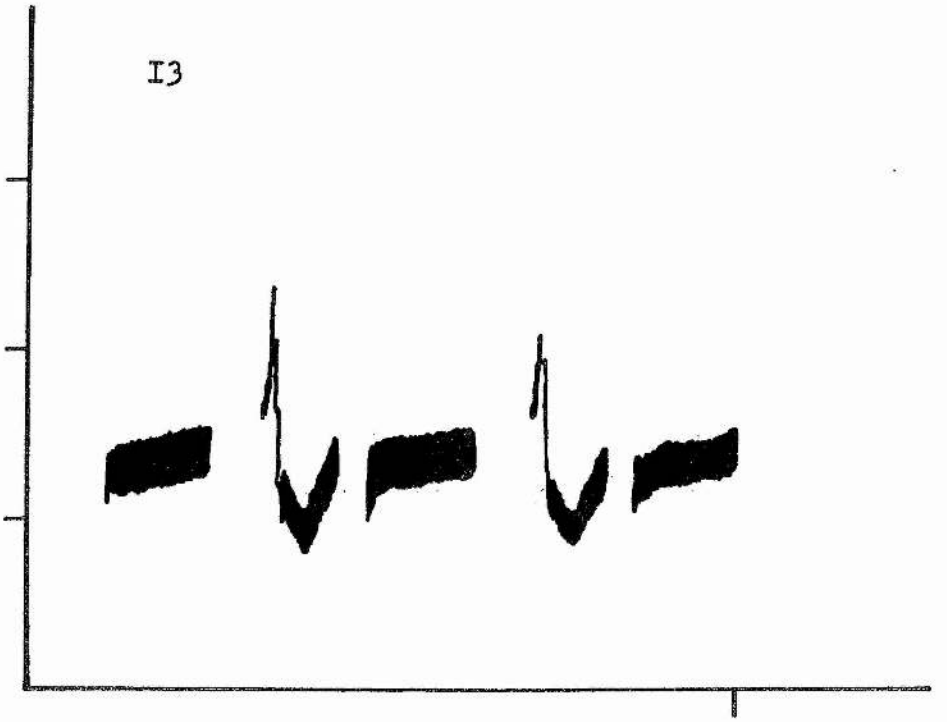
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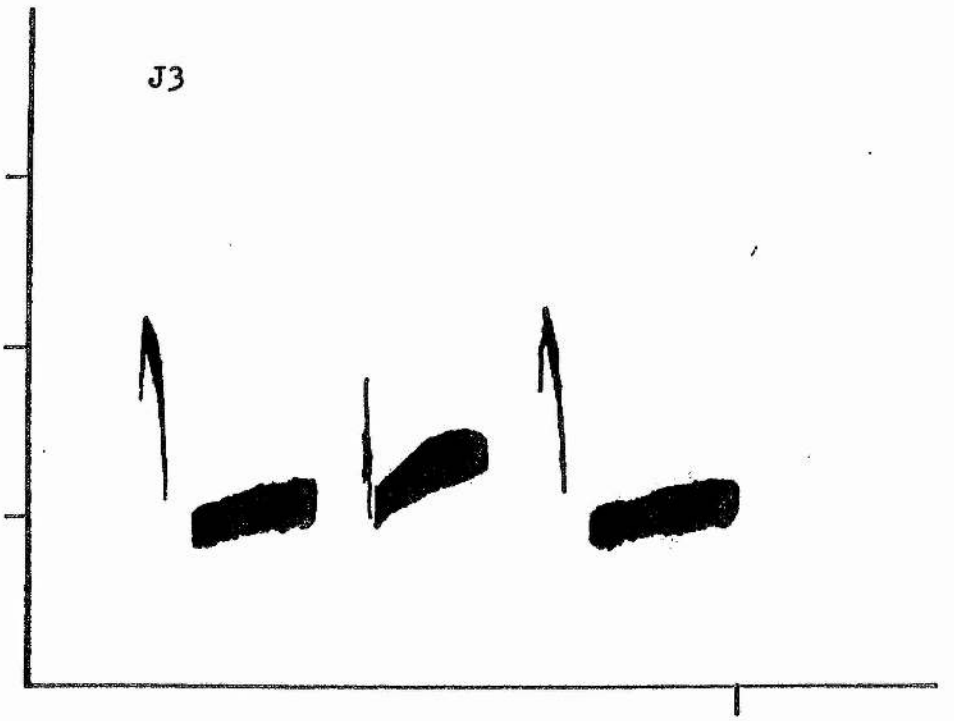
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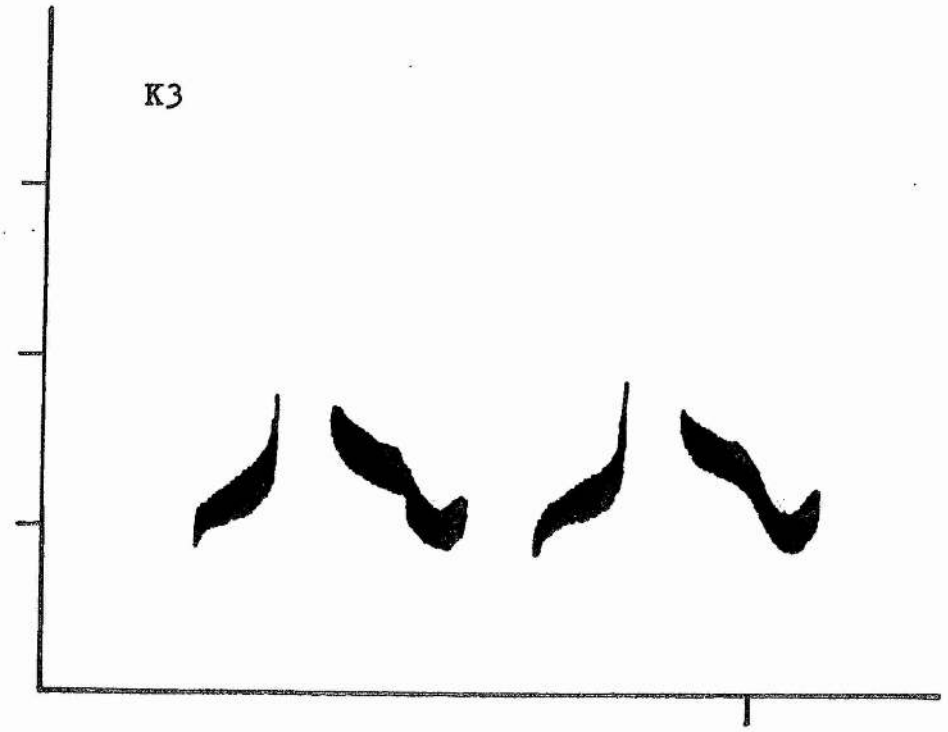
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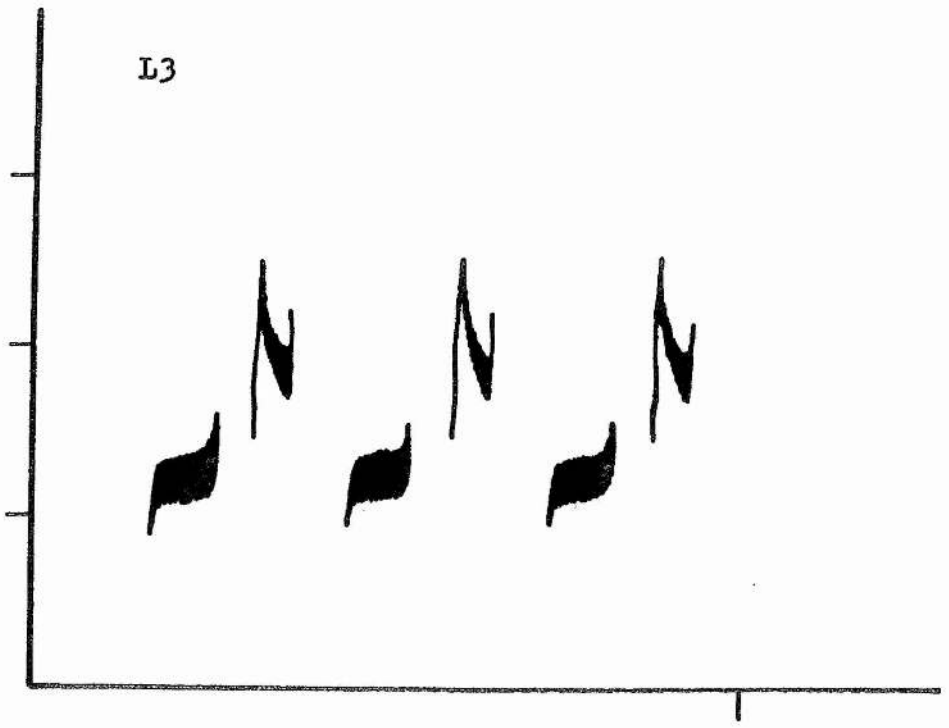
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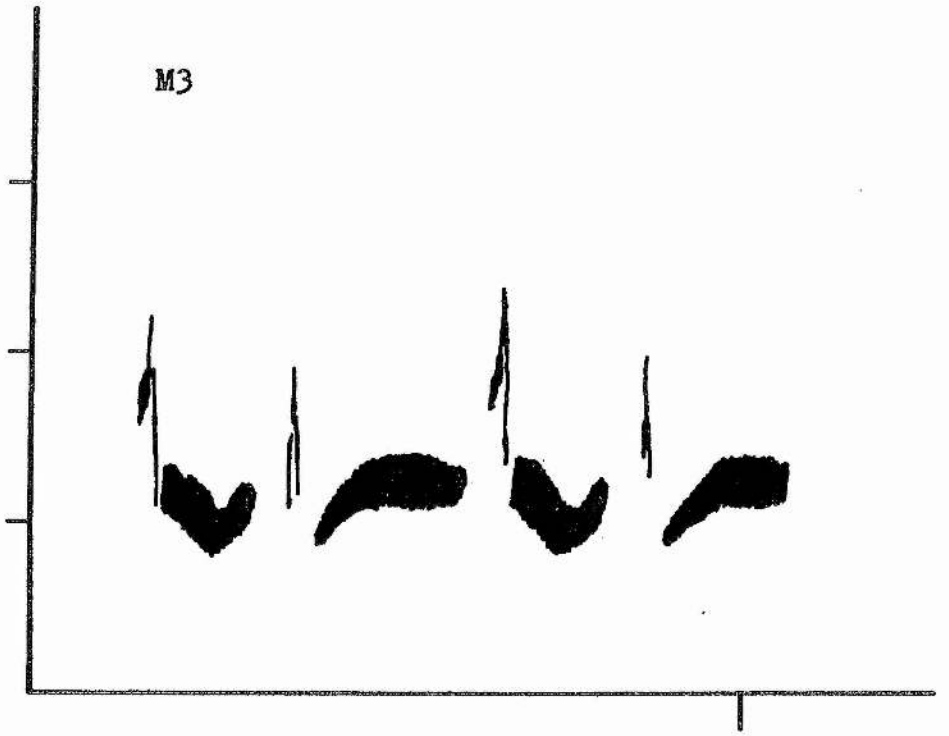
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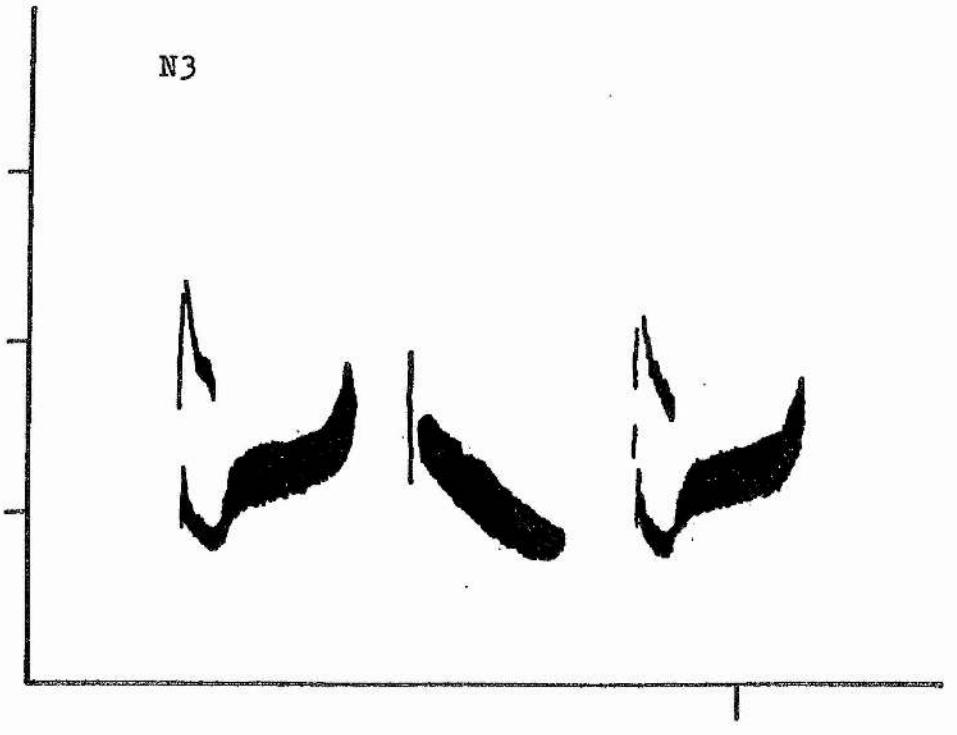
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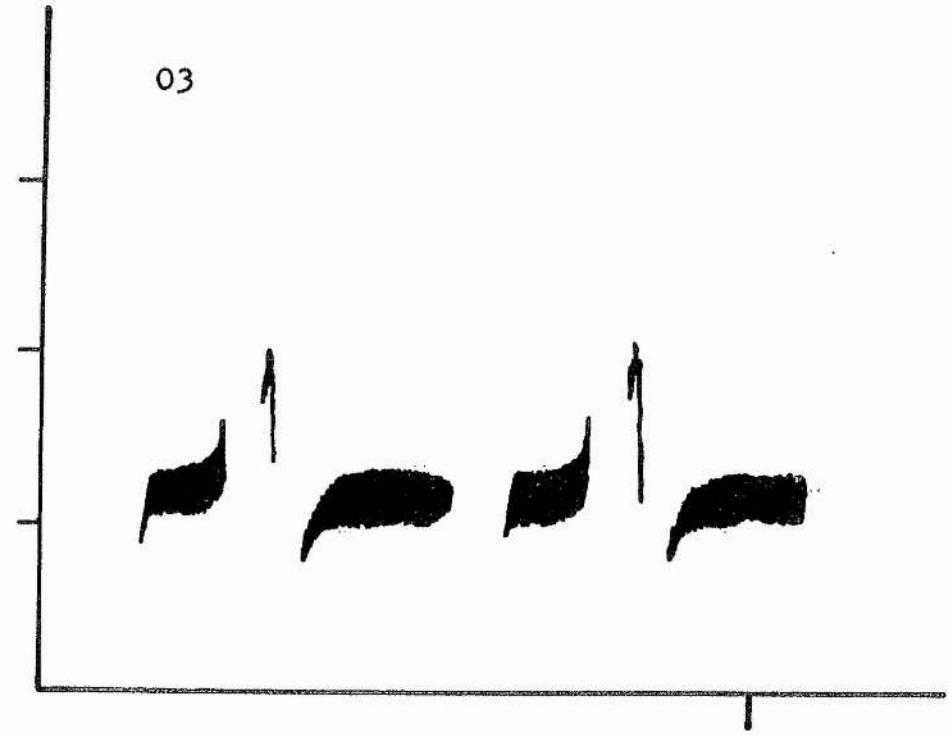
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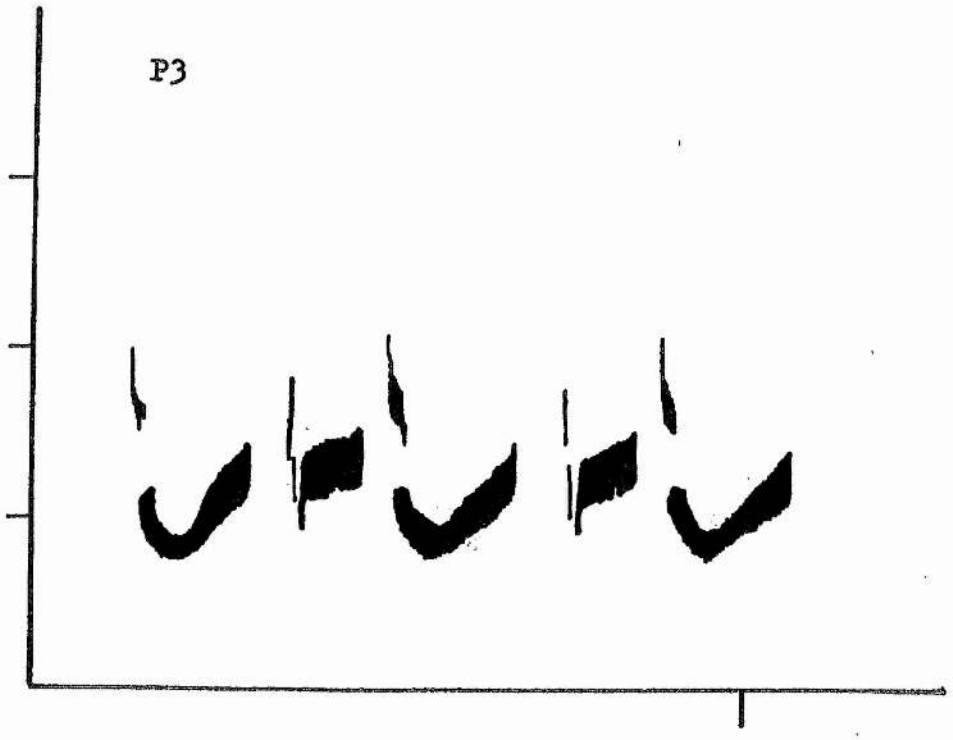
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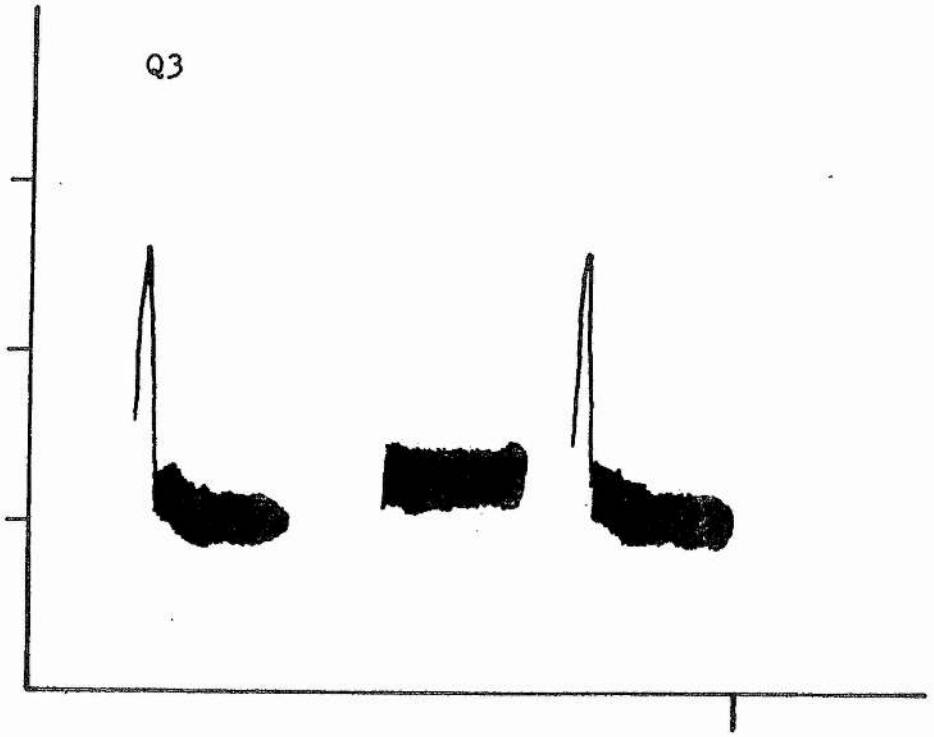
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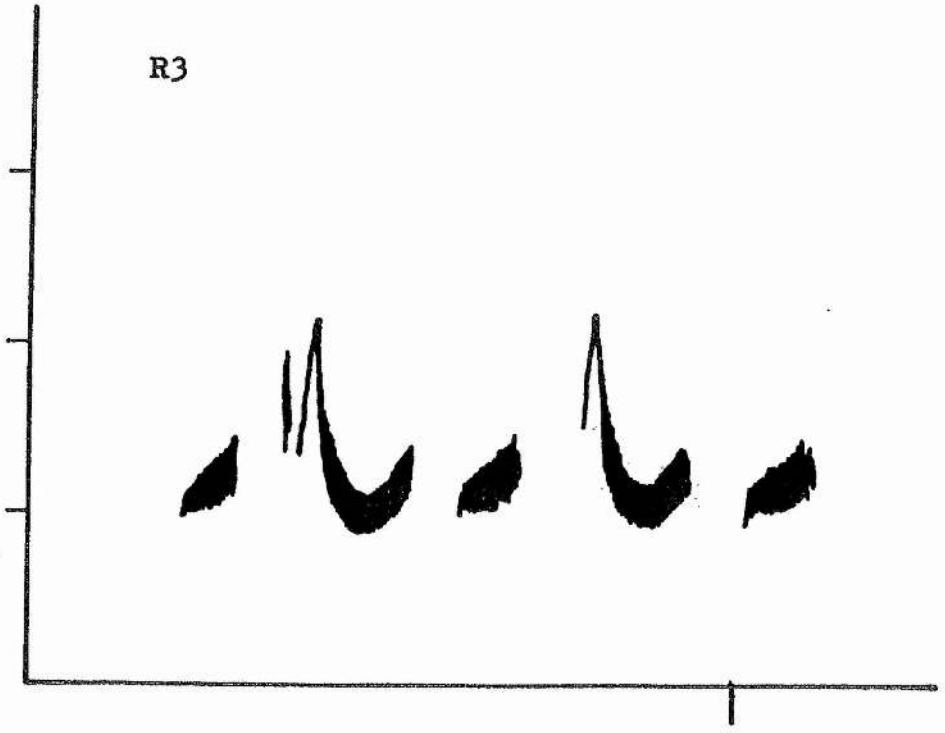
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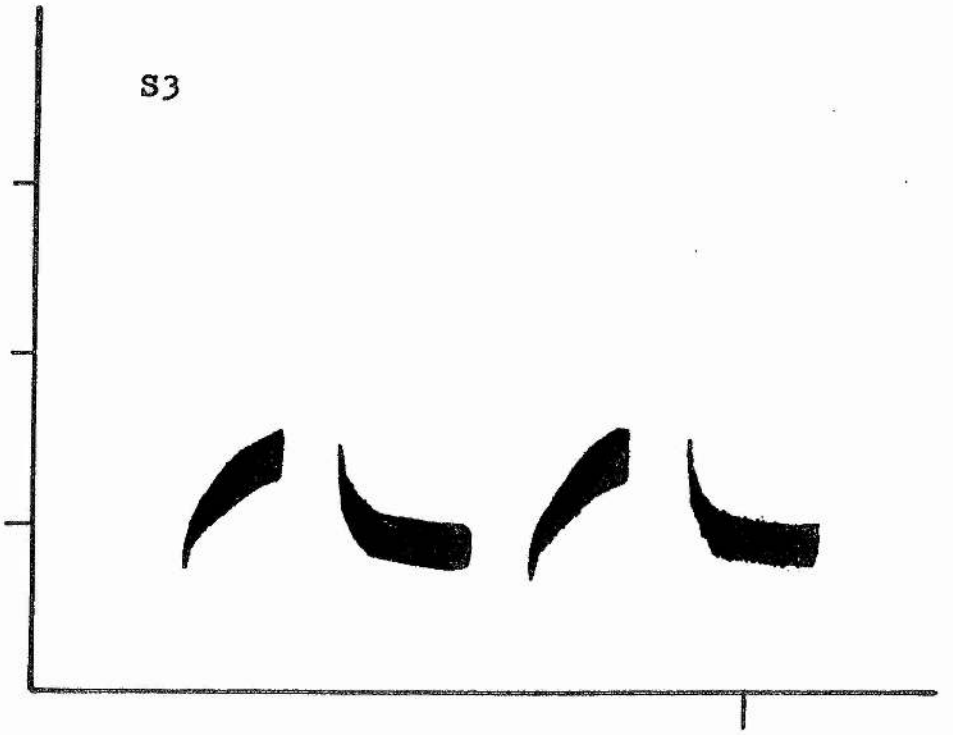
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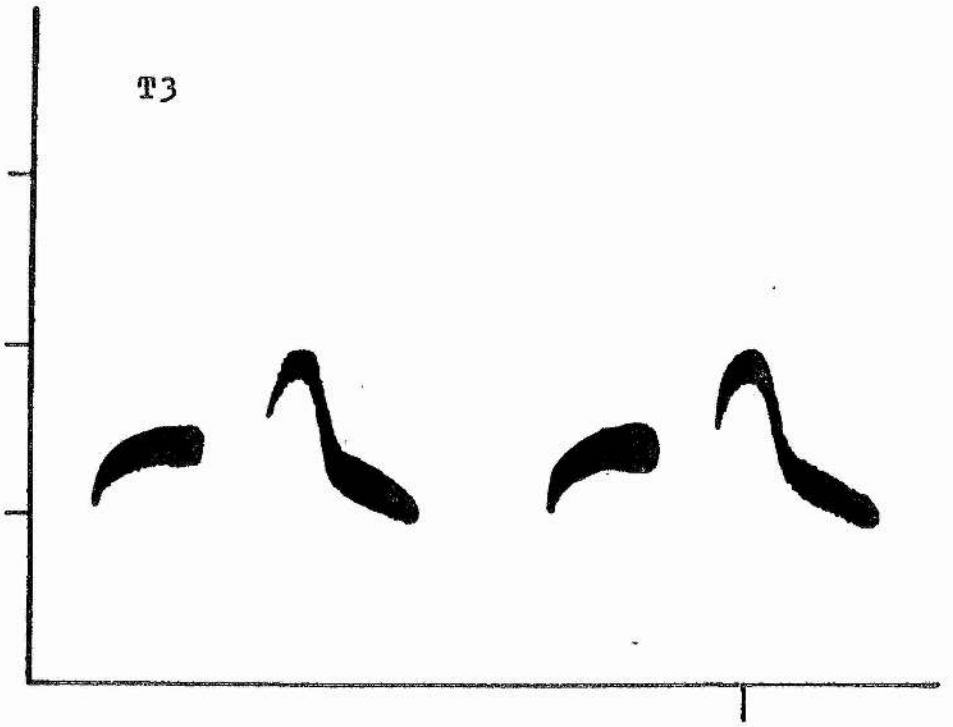
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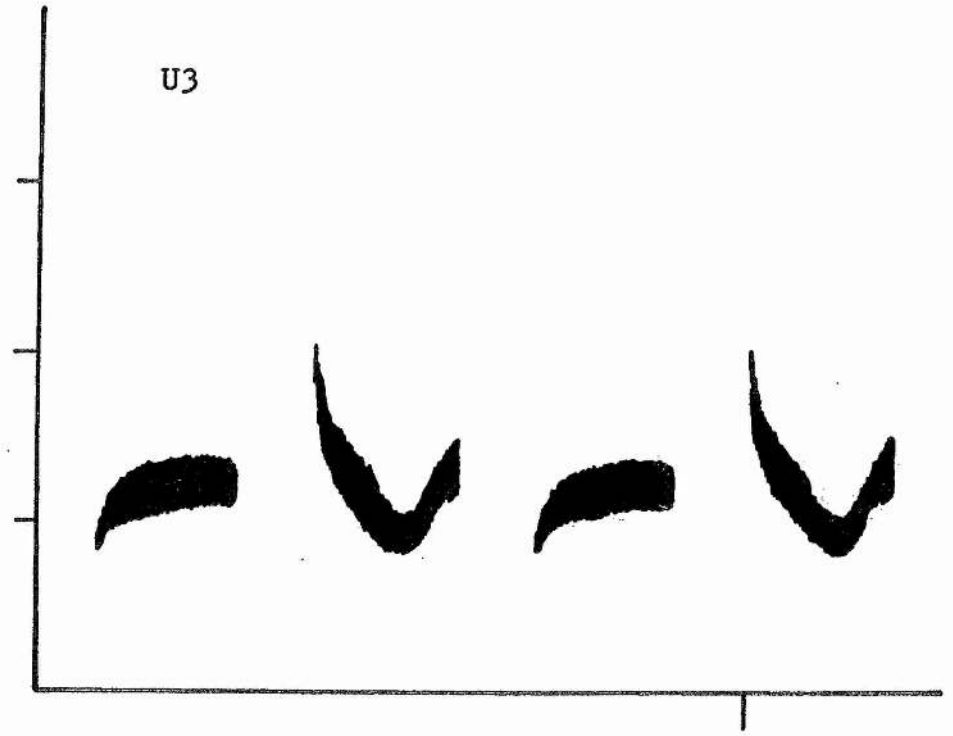
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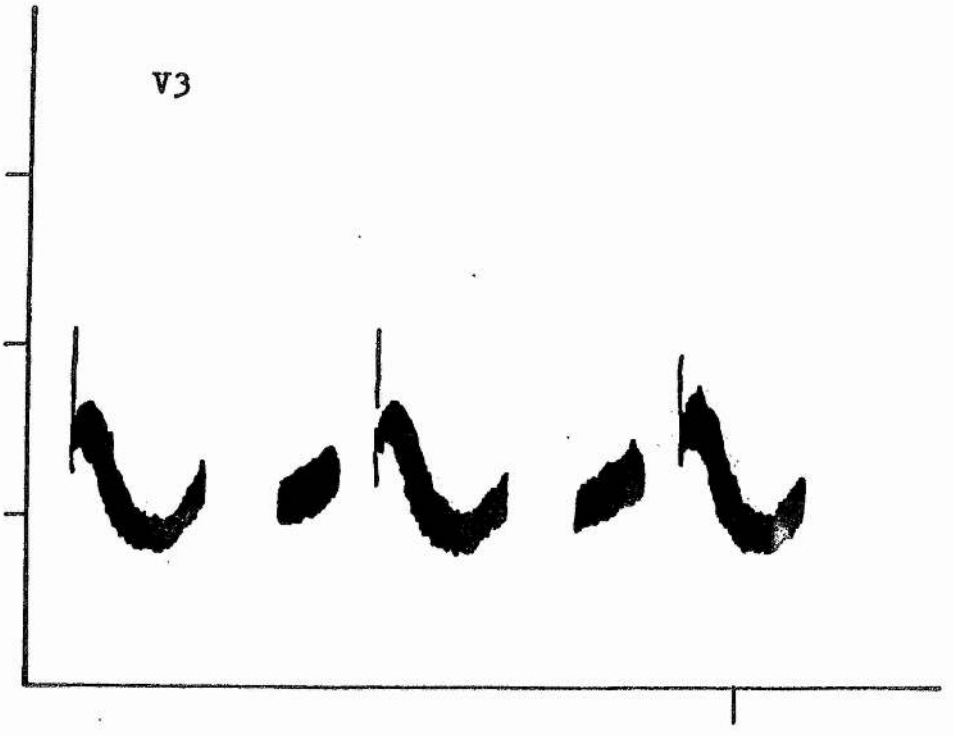
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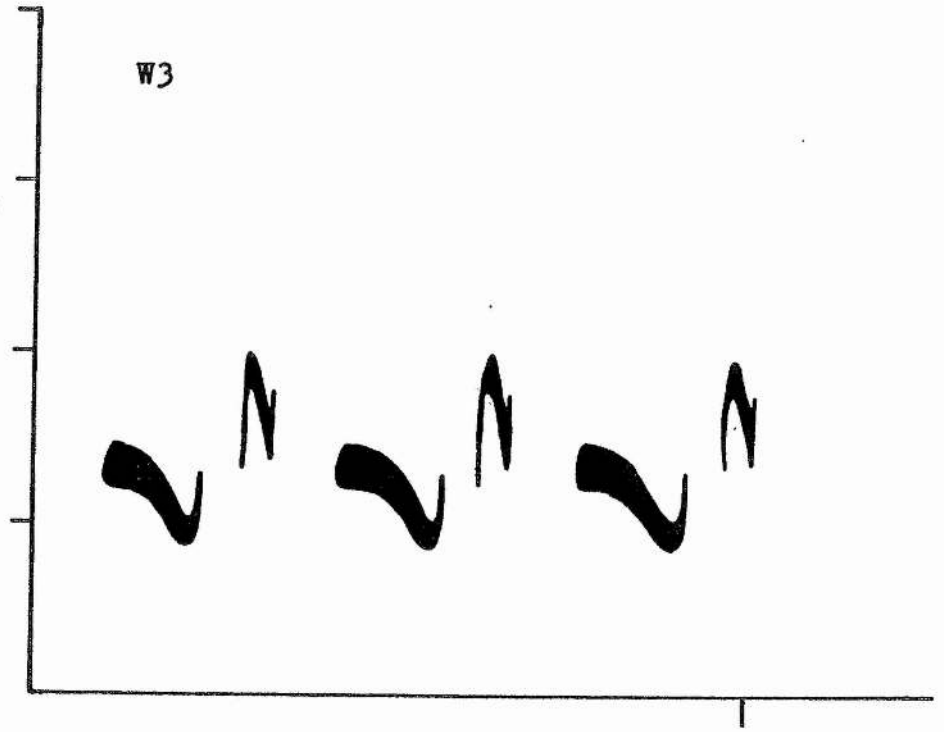
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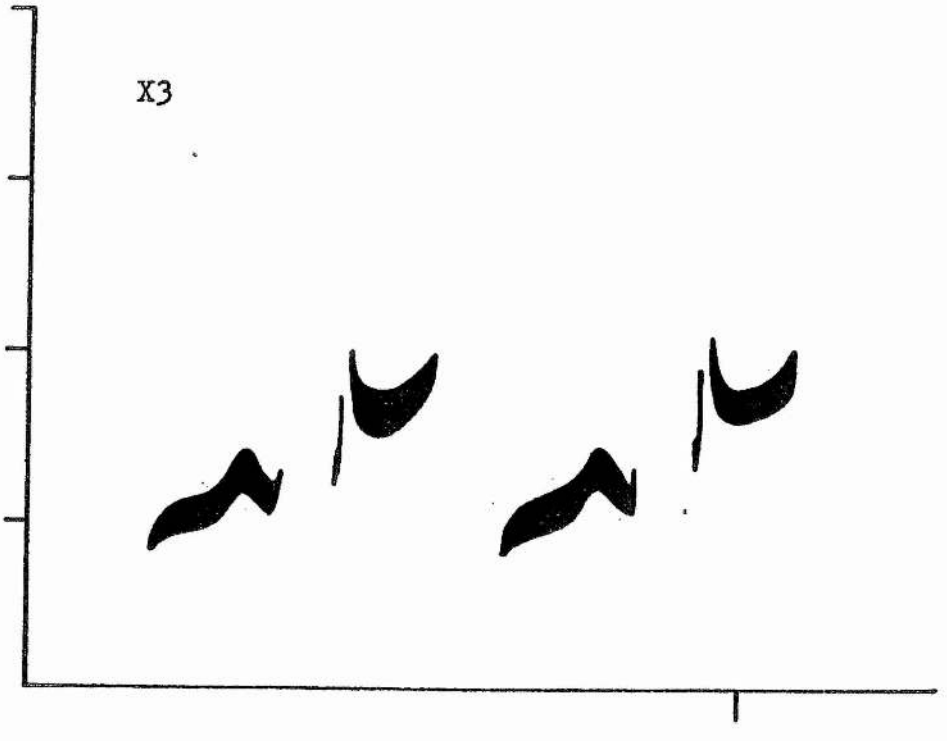
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Appendix 2.1. A worked example of estimating the number of song types within a coal tit population at Tentsmuir, using the 'capture-recapture' method (Schnable's method).

THE METHOD.

Schnable's capture-recapture method is a method for estimating a population of an organism. Brower & Zar (1977) suggested that the following assumptions must be met for this method to be valid:

(1) All individuals in the populations must have an equal and independent chance of being captured. That is, the samples taken are random.
(2) The ratio of marked to unmarked organisms must not change. That is, there should be no significant addition of new organisms into the population. In other words, the size of population must be constant.
(3) All individuals, marked or unmarked, must have the same opportunity for being captured. That is, they distribute themselves randomly.

Having established these assumptions, and carried out the observations, the population (N) is estimated using the following formula :

$$N = \Sigma\, n_i M_i \;/\; \Sigma\, R_i$$

where M_i is the total number of marked individuals in the population prior to day i, n_i is the number of animals caught

in the sample on that day, and R_i is the number of recaptures caught on that day.

AN EXAMPLE.

The following table shows hypothetical data collected for Schnable population estimation (taken from Brower & Zar 1977).

Day (i)	Number in sample on day i	No.of Recaptures (R_i)	No.of newly marked	Total no. previously marked (M_i)	n_iM_i
1	40		40		
2	44	9	35	40	1760
3	38	14	24	75	2850
		$\Sigma R_i = 23$			$\Sigma n_iM_i = 4610$

The estimated population (N) $= \Sigma n_iM_i / \Sigma R_i$

$= 4610 : 23$

$= 200$

APPLICATION TO SONGS FROM TENTSMUIR.

An analogous application can be made to the songs of a coal tit population at Tentsmuir.

Song types recorded each year can be identified as the number of samples in each year, which are '**marked**' and '**released**' into the '**population**' of song types.

Song types which had been recorded in year 1 and were re-recorded in year 2 can be identified as the number of recaptures.

Song types which were not recorded in previous years are the number of newly '**marked individuals**'.

The total song types which were recorded in a year were the total number of 'marked individuals', or the total number of song types recorded that year plus that recorded in previous year.

Similar assumptions can be made for the songs at Tentsmuir, that : (1) song types recorded each year are random samples, (2) the number of song types present in a population of coal tits at Tentsmuir is roughly constant, and (3) all song types are equally likely to be recorded.

The following table shows the observed data during 1989-1991:

Year (i)	Number in sample on year i	No.of Recaptures (R_i)	No.of newly marked	Total no. previously marked (M_i)	n_iM_i
1989	31		31		
1990	49	25	24	31	1519
1991	22	18	4	55	1210
		$\Sigma R_i = 43$			$\Sigma n_iM_i = 2729$

The estimated number of song types present in the population

$$N = \Sigma n_iM_i \; / \; \Sigma R_i$$

$$= 2729 : 43 = 63$$

This is, however, only a rough estimate of the number of song types that might be present in the coal tit population at Tentsmuir. The rate of change of song types was estimated using this estimate.

REFERENCE.

Brower,J.E. & Zar,J.H. 1977. ***Field and Laboratory Methods for General Ecology***. WM.C.Brown Co.Publs., Iowa, USA. pp. 98-101.

Appendix 2.2. Worked example of estimating total loss and gain of song types in Tentsmuir 1990-1991.

1) Recorded Song Types :

1989 --	Newly recorded	= 31 song types
1990 --	Recorded in 1989	= 25 song types
	Newly recorded	= 24 song types
1991 --	Recorded in 1989	= 5 song types
	Recorded in 1990	= 13 song types
	Newly recorded	= 4 song types

2) Total Loss in 1990 : 31 - 25 = 6 song types
= 6 : 63
= 9.52 %.

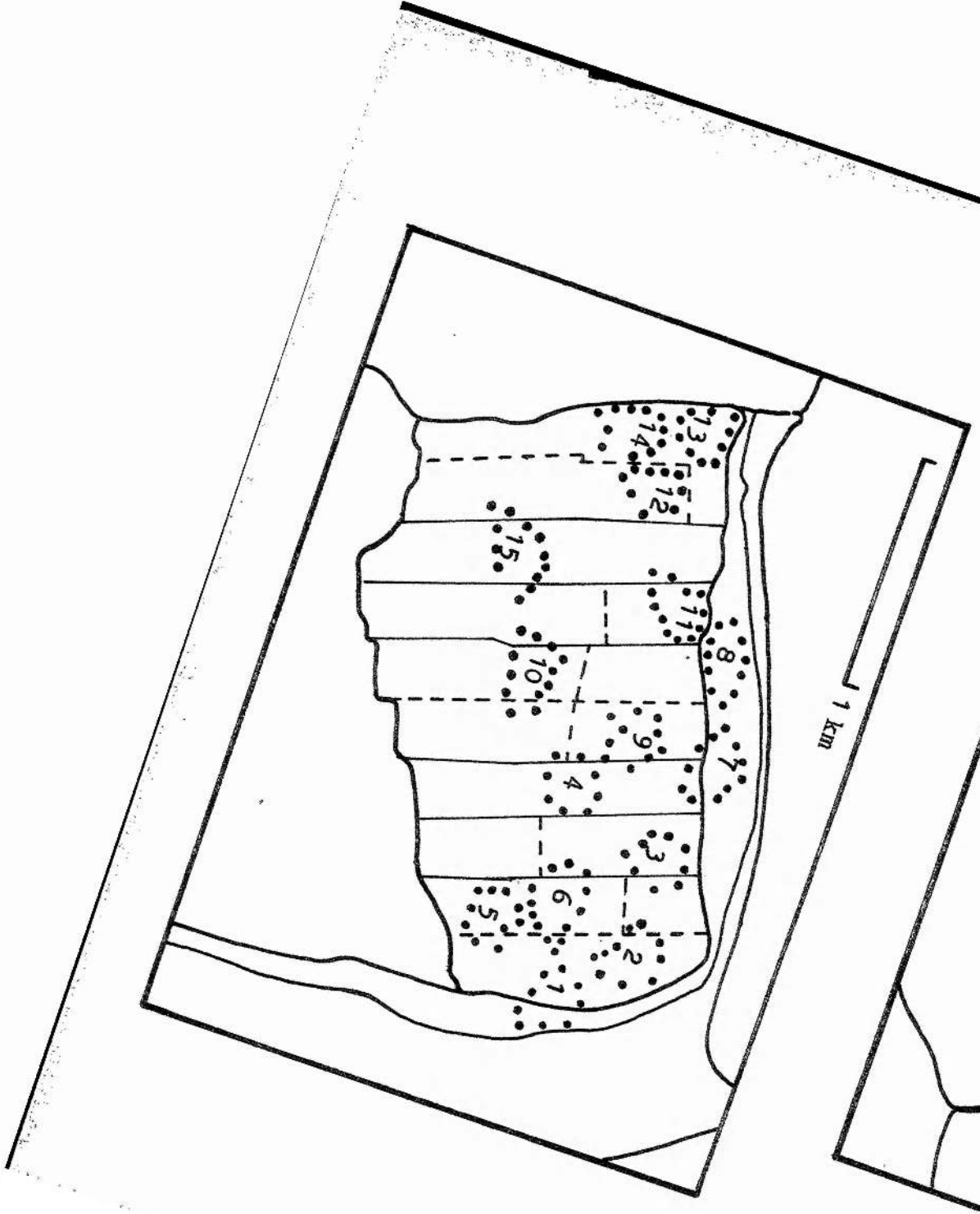
Total Gain in 1990 : 24 song types
= 24 : 63
= 38.09 %.

3) Total Loss in 1991 : (31-5)+(24-13) = 37 song types
= 37 : 63
= 58.73 %.

Total Gain in 1991 : 4 song types
= 4 : 63
= 6.35 %.

4) Average Loss = (9.52 + 58.73) : 2 = 34.12 %.
Average Gain = (38.09 + 6.35) : 2 = 22.22 %.

Note : 63 is the estimated total song types available in the population.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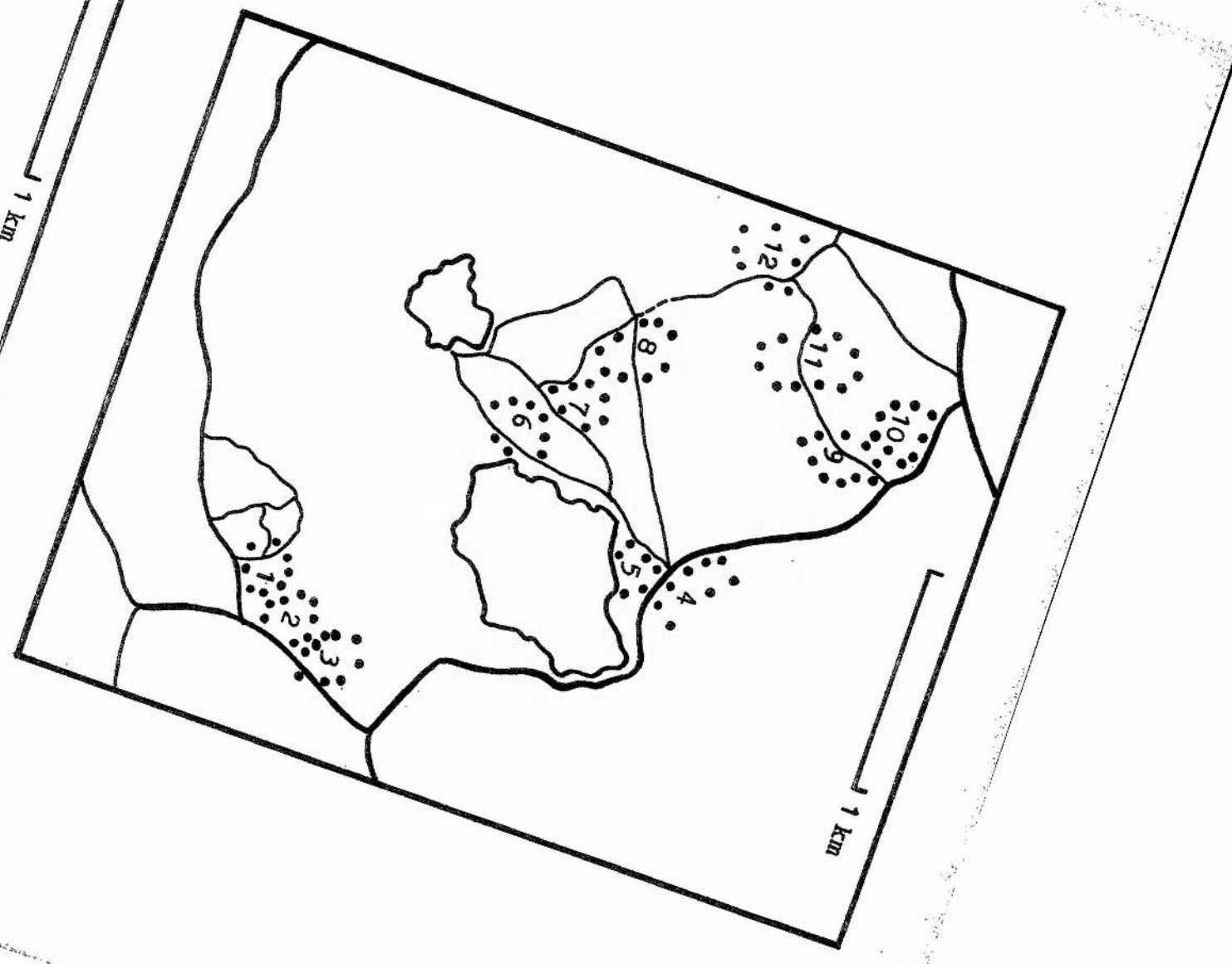
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